Overwinter Survival of Juvenile Atlantic Cod (*Gadus morhua*) in a Coastal Ecosystem

by

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A Thesis submitted to the School of Graduate Studies

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Biology

Memorial University of Newfoundland and Labrador

October 2022

St. John’s, Newfoundland and Labrador

Abstract

Acknowledging poor understanding of natural mortality in juvenile fish, especially throughout first winter, I synthesized past studies that suggest that physiological and metabolic stress in the first winter result in a critical survival period that determines cohort strength. Juvenile Atlantic cod (*Gadus morhua*) in coastal Newfoundland settle in nearshore habitats in 3-6 pulsed events each year, creating a broad size-structured age-0 year-class with potentially different survival trajectories entering their first winter. To assess size-specific survival across winter, I classified age-0 and age-1 pulse structure using finite mixture distribution models. I evaluated juvenile cod survey data and archived juvenile cod samples with winter temperature records to determine effects of winter duration, body condition, and settlement time on overwinter survival. Higher condition entering winter and smaller size combined with earlier fall settlement all improved overwinter survival among pulses. Increased body condition in the fall, and earlier settlement timing among pulses aligned with high fall temperatures. I further investigated the role of body size and condition on overwintering success through feeding trials at ambient overwinter sea temperatures, using demersal age-0 cod collected from Newman Sound, Newfoundland. I showed that small amounts of consumed food (<1% body weight · d^{-1}) maximized winter growth and condition potential of juvenile cod in Newfoundland waters. I also used capture-mark-recapture and condition metrics to evaluate in situ winter movement and survival of age-0 cod in Newman Sound. Highest fall mortality characterized late settling juveniles relative to early settling juveniles (16.20%·d^{-1} vs. 4.52-7.72%·d^{-1}), noting unexpectedly low overwinter mortality in the first two groups (0.0052 and 0.0022%·d^{-1}). My research highlights the importance of food prior to and during winter to promote energy reserves for survival in the first year of life. These combined studies demonstrate potentially low winter mortality in early settling juveniles and emphasize the critical importance of the period leading up to winter for survivorship, with increased resources before and during winter reducing a survival bottleneck. These findings advance the understanding of overwinter survival and recruitment in sub-arctic marine ecosystems in a changing climate and challenge many assumptions of high overwinter mortality in sub-arctic cod populations.

Acknowledgements

This research would not have been possible without the support and involvement of many people. First, I would like to thank both of my supervisors, Bob Gregory and Paul Snelgrove. Bob taught me to ask critical research questions and have confidence in my work. Paul taught me how to communicate effectively, whether through writing or presentations. I have learned from both of my supervisors that science needs to be shared and communicated with purpose and passion. I also thank my committee member, Ben Laurel. He went above and beyond, providing guidance from the beginning until the end. Ben taught me how to think critically and was always available to discuss ideas on analyses and results.

This PhD would not have been possible without the tireless efforts of the DFO Terra Nova Field Crew. A special thanks to Brianna Newton, who helped me prepare for field work and fulfilled endless data requests. Another special thanks to Kate Dalley, who led field work during my tagging study. A thanks to Phil Sargent for helping me collect juvenile cod for experimental work. Lastly, thank you Chelsea Bloom for all your support and help throughout our condition study.

To everyone at OSC – I wouldn’t trade it for anything. Special thanks to: JoAnn, for always helping me with paperwork; Christine Vickers, for helping keep my experimental fish happy and healthy; Chris Canning, Damien Whitten, and John Evely and everyone at OSC Laboratory Services for your help with tank room facilities and water management. Finally, thank you Danielle Nichols – OSC would not be the same without you.

Terra Nova National Park provided access to facilities. Funding was provided by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans

Canada and INREST (representing the Port-of-Sept-Îles and City of Sept-Îles), as well as the School of Graduate Studies and Memorial University. Travel to conferences, meetings, and workshops were provided by NSERC Canadian Healthy Oceans Network, Memorial University, US National Science Foundation, and the Scientific Committee on Oceanic Research.

I am also grateful for all the members of the Snelgrove Lab. A special shoutout to Emma Cooke and Evelyn MacRobert – we were quite the team! Marta, Alessia and Ben – our time in the office together was the perfect balance of work and fun. Lastly, a thanks to Neus, who always provided guidance when I had lab and writing questions.

Finally, I sincerely thank my family and friends for their unwavering support. To my parents – thank you for your endless love and support. To my friends, this would not have been possible without you – from Yellowbelly Trivia to Team Slow Clap to Saturday dives in Brigus – you all created a wonderful environment outside of work. Finally, I wouldn't have made it to the end without my biggest advocate, Ian. Thank you for all you do.

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Co-authorship statement

The research detailed in this thesis was designed and conceptualized by Emilie Geissinger in collaboration with supervisors Drs. Robert Gregory and Paul Snelgrove and with assistance from committee member Dr. Benjamin Laurel. All data were collected, analyzed, and interpreted by Emilie Geissinger, and all manuscripts resulting from this research were written by Emilie Geissinger. Dr. Robert Gregory assisted with field work and sample collection. Drs. Robert Gregory, Paul Snelgrove, and Benjamin Laurel provided assistance with delineating the content and structure of Chapter 1-7, along with editing assistance.

Specific contributions for Chapter 2-6 are listed below:

Chapter 2: This chapter was inspired by the review topic for Emilie Geissinger's comprehensive exam at Memorial University. Emilie Geissinger built on this initial review by developing the research questions and objectives, reviewing relevant literature, collecting mortality rates from peer-reviewed publications, and writing the manuscript, with editorial assistance from Drs. Paul Snelgrove and Robert Gregory.

Chapter 3: Emilie Geissinger conceptualized the research questions and conducted the statistical analyses for pulse assignments with guidance and input from Dr. Robert Gregory. Emilie Geissinger wrote the chapter with editorial assistance from Drs. Paul Snelgrove and Robert Gregory.

Chapter 4: Chelsea Bloom initiated work on the role body condition has on abundance of juvenile Atlantic cod post-winter for her BSc Honours thesis. Emilie Geissinger further developed this work to incorporate winter duration and condition by pulse structure in relation to survival probability. Assistance on analysis and interpretation was provided by Drs. Benjamin Laurel, Paul

Snelgrove, and Robert Gregory. The publication and chapter were written by Emilie Geissinger, with editorial assistance from Chelsea Bloom, Drs. Benjamin Laurel, Paul Snelgrove, and Robert Gregory. This chapter is under review in *Marine Ecology Progress Series*.

Chapter 5 and 6: Emilie Geissinger, Drs. Robert Gregory, and Paul Snelgrove conceptualized research questions. Emilie Geissinger, Drs. Robert Gregory, Paul Snelgrove, and Benjamin Laurel developed experimental design. Emilie Geissinger and Dr. Robert Gregory conducted field work. Emilie Geissinger completed laboratory work (Chapter 5), otolith analysis (Chapter 6), condition measurements, and statistical analyses. Emilie Geissinger wrote the chapters with comments and revisions by Drs. Robert Gregory, Snelgrove, and Benjamin Laurel. Chapter 5 was published in *Canadian Journal of Fisheries and Aquatic Sciences* in 2021 and Chapter 6 was published in *ICES Journal of Marine Science* in 2022.

Chapter 1 – Natural mortality in the juvenile gadid life stage

1.1 Background

Complex and variable natural mortality occurs throughout the juvenile phase of fishes and throughout seasons. Given high variation, processes that occur in young juveniles – i.e., between age-0 and age-3 – may heavily influence year-class strength (*Pseudopleuronectes americanus*, Tyler *et al.*, 1997; *Gadus morhua*, Bogstad *et al.*, 2016). Many studies have estimated natural mortality rates for egg, larval, and adult life stages in aquatic systems. The juvenile life stage provides a particular challenge because juvenile fishes provide an unclear numerical link between larval and adult life stages (Stige *et al.*, 2013). Seasonal variation in juvenile survival (*Lateolabrax japonicus*, Shoji and Tanaka, 2007; *Centropomus undecimalis*, Barbour *et al.*, 2014) exacerbates the challenge of linking early life stages to adult life stages. Intensive research on juvenile fishes has produced long time-series data (Nash and Geffen, 2012; Ottersen *et al.*, 2014; Lunzmann-Cooke *et al.*, 2021; Litzow *et al.*, 2022). However, the inherent environmental and biological variation in natural mortality rates across species and regions limit calculations of mortality rates to individual populations, rather than species (e.g., cod). Focused research on juvenile natural mortality can promote a better understanding of population dynamics in aquatic systems.

The juvenile stage provides a critical transition from the larval stage, often involving habitat changes along with a shift in food sources (Grant and Brown, 1998; Ottersen *et al.*, 2014) that result in variable mortality in the juvenile stage. Furthermore, density-dependent mortality can impact juveniles (Myers and Cadigan, 1993), in contrast to assumed density independent effects on egg and larval stages (Myers, 2001). For example, previous work predicts instantaneous mortality rates in demersal Northeast Arctic juvenile cod between 0.01 and 0.03 day^{-1} (Bogstad *et al.*, 2016), contrasting an instantaneous mortality rate of 0.068 day^{-1} for age-1 Atlantic cod as well as 0.021 day^{-1} for age-0 Greenland cod (*Gadus macrocephalus ogac*) in Newfoundland (Sheppard, 2005). In coastal Gulf of Alaska, post-settlement mortality in gadids ranges from 22-90% losses over a 5-6 week period (Laurel *et al.*, 2016). Multiple studies emphasize the influence of size on natural mortality in juvenile fishes (Kristiansen *et al.*, 2000; Stige *et al.*, 2019), as well as growth (Laurel *et al.*, 2016, 2017), energetics (Finstad *et al.*, 2004; Abookire *et al.*, 2022), predation (Kristiansen *et al.*, 2000; Ciannelli *et al.*, 2007), and temperature (Hurst *et al.*, 2012; Ottersen *et al.*, 2014).

1.1.1 Size and growth

Growth rates and settlement size vary strongly and annually among juvenile fish populations, such as in Pacific cod (*G. macrocephalus*), saffron cod (*Eleginus gracilis*), and walleye pollock (*G. chalcogrammus*; Laurel *et al.*, 2016). Rapid growth between settlement and the first overwintering period can lead to higher survival in coastal cod. However, weaker recruitment signals link with low growth potential in cold winters (Laurel *et al.*, 2017), but overwinter growth can occur if food is available (Geissinger *et al.*, 2021). Larger size also promotes higher survival (Kristiansen *et al.*, 2000; Geissinger *et al.*, 2022), with positive associations between size and age-1 abundance (Stige *et al.*, 2019).

1.1.2 Energy storage

Insufficient energy stores increase predation risk in juvenile fishes (*Oncorhynchus mykiss*; Mogensen and Post, 2012), and also increase starvation risk (Geissinger *et al.*, 2021). For example, juvenile Atlantic herring (*Clupea harengus*) shift from a protein-based growth to lipid storage when they reach a certain length before the first winter (Sewall *et al.*, 2019). In Atlantic salmon (*Salmo salar*), increased risk during winter elevates the importance of energy stores before and during winter (Finstad *et al.*, 2004). Higher body condition when juvenile cod enter winter increases survival probability (Geissinger *et al.* 2022, *submitted*). These observations strongly suggest that lipid energy accumulation in the summer and fall period may influence overwinter survival in juvenile cod (Copeman *et al.*, 2016; Abookire *et al.*, 2022).

1.1.3 Predation

Availability of refuge habitat plays an important role in levels of predation (Lundvall *et al.*, 1999). Habitat complexity allows juvenile fishes to seek refuge from predation (Gotceitas *et al.*, 1995; Lindholm *et al.*, 1999). In coastal Newfoundland, age-0 cod strongly associate with eelgrass (Gotceitas *et al.*, 1997) as a means to avoid predation (Linehan *et al.*, 2001). Higher predation rates occur in fragmented habitats, with increased predation risk in small patches (Laurel *et al.*, 2003a). Furthermore, predation risk on age-0 cod depends on patch size and patch edges, with highest risk in intermediate sized patches (Gorman *et al.*, 2009). As the leading cause of natural mortality in juvenile fishes (Sogard, 1997), population assessments must consider predation when assessing mortality risks.

1.1.4 Temperature

Temperature plays an important role in recruitment in juvenile fishes, with strong climate events leading to recruitment failures (Litzow *et al.*, 2022). Evidence indicates that some juveniles actively select habitat based on temperature (Hurst *et al.*, 2012). Temperature also influences links between size and abundance in Atlantic cod (Ottersen and Loeng, 2000); however, weak correlations limit our capacity to estimate abundances at later life stages based on age-0 indices (Ottersen and Loeng, 2000). Regardless of the weak correlation, temperature also strongly influences recruitment (Ottersen *et al.*, 1994). Additionally, temperature influences food availability; warm and cold conditions affecting zooplankton species composition, energy content, and abundance (Siddon *et al.*, 2013).

1.2 Thesis Summary

Numerous studies have focused on juvenile fish ecology in coastal Newfoundland. An ongoing 26-year coastal juvenile seining program (Gregory *et al.*, 2019) has provided opportunities to study habitat use (Laurel *et al.*, 2003b; Renkawitz *et al.*, 2011), pulse structure (Ings *et al.*, 2008), predation (Linehan *et al.*, 2001; Gorman *et al.*, 2009) and movement (Shapiera *et al.*, 2014) of juvenile cod. The coastal juvenile seining program has highlighted the transition from age-0 to age-1 cod as an important recruitment process (Laurel *et al.*, 2017; Lunzmann-Cooke *et al.*, 2021). The challenges in sampling juvenile fish overwinter and lack of long-term datasets result in a dearth of studies on overwinter survival in seasonal environments and particularly in sub-arctic marine juvenile fishes. Differences in intra-annual survival rate within populations represents a critical knowledge gap in recruitment dynamics, and overwinter survival was considered a potential critical component in structuring population abundance (Fullerton *et al.*, 2000; Mogensen and Post, 2012). However, my research has shown that winter is not a survival bottleneck, and winter survival can be high given the right circumstances (i.e., food, Geissinger *et al.*, 2021; size, Geissinger *et al.*, 2022; condition, Geissinger *et al., in review*).

Many freshwater studies have addressed overwinter dynamics in juvenile fishes (e.g., Fullerton *et al.*, 2000; Pangle *et al.*, 2004; Brakensiek and Hankin, 2007). Winter survival can increase with increased body size in some juvenile fishes (Hunt, 1969; Pangle, 2004). However, body size in isolation does not always determine winter survival. Size-structured mortality in largemouth bass (*Micropterus salmoides*) juveniles is only evident in the presence of predators (Garvey *et al.*, 1998). Predators therefore play an important role in behavior and survival

(Abrahams and Dill, 1989; Anderson, 2001). Largemouth bass can gain mass and energy in the absence of predators but only maintain mass and energy following the introduction of predators. The role of body size on winter survival links strongly with energetics. When food is available, larger juveniles tend to fare better than smaller juveniles (Thompson *et al.*, 1991; Pangle *et al.*, 2004). Cold temperature can further increase effects of food on fish energetics. For example, rainbow trout (*Oncorhynchus mykiss*) experience low survival (approximately 6% of fish surviving winter) in cold, resource limited lakes, attributed to small size and low lipid levels, whereas exceeding high survival can occur in warm, high resource lakes, with approximately 82% of fish surviving winter (Mogensen and Post, 2012).

Winter temperature and duration can also strongly affect winter survival, with temperature often contributing to variation in food consumption in largemouth bass (Fullerton *et al.*, 2000). Colorado squawfish (*Ptychocheilus lucius*) exhibit limited growth and decreased condition throughout winter regardless of food availability, with condition declining more during longer winters (Thompson *et al.*, 1991). A simulation study showed that annual mortality of yellow perch (*Perca flavescens*) ranged from 20% during short winter durations with large body size, to 63% during long winters with small body size (Post and Evans, 1989). These results indicate that severe winters can significantly contribute to energy depletion in freshwater fishes.

Despite extensive research on freshwater winter survival, whether freshwater processes translate to marine ecosystems remains unclear. Freshwater studies occur in effectively closed systems (e.g., within an individual lake or pond), greatly simplifying efforts to understand predator abundance and food availability. In contrast, the open nature of marine systems adds complexity and necessitates inferences based on incomplete information about specific survival processes. Sub-arctic marine waters, with their seasonal variation, long, cold winters and short, mild summers, create a particular challenging environment for population dynamics research. Atlantic cod settle from an open water pelagic environment to a seabed-associated juvenile stage during several pulses throughout summer and fall (Methven and Bajdik, 1994; Ings et al 2008), resulting in multiple-mode size frequencies for age-0 Atlantic cod entering winter. In other size-structured populations, individual growth rates play a central role in determining population trajectories (Werner and Gilliam, 1984). Temperature and food availability limit growth rates through winter (Grant and Brown, 1999; Geissinger *et al.*, 2021), and the size of an individual going into winter may therefore determine its survival, with large fish usually faring better than smaller individuals (Sogard, 1997).

1.3 Objectives

Few studies have documented the effects of habitat, food, temperature, and growth on overwinter survival of juvenile marine fish. My research focuses on 7 objectives, by combining statistical modeling, experimental techniques, and field studies to determine factors that limit overwinter survival. The specific aims are to:

- Synthesize past research on natural mortality in marine fishes across life stages, to identify key gaps and potential pathways forward (Chapter 2).
- Characterize pulse structure from age-0 to age-1 Atlantic cod using finite mixture distribution models and seining data (Chapter 3).
- Evaluate overwinter size-structured mortality in age-0 cod based on recruitment pulses (Chapter 4, 5, and 6).
- Investigate the role of winter duration in overwinter mortality using 18 years of field data (Chapter 4).

- Evaluate the role of body condition in overwinter mortality using long-term field data and a laboratory study (Chapter 4 and 5).
- Evaluate the role of food availability (starvation, low, medium, and high ration) in winter growth and survival in the laboratory (Chapter 5).
- Estimate overwinter dispersal and mortality in a field-based capture-mark-recapture study (Chapter 6).

In Chapter 2, "Natural morality rates of fishes in the ocean: a review across multiple life stages", I review natural mortality rates of marine fish in the egg, larval, juvenile, and adult stage. The chapter compares approaches to estimating natural mortality and evaluates variation between species within each life stage.

In Chapter 3, "Recruitment of age-0 and age-1 Atlantic cod (*Gadus morhua*) in a coastal ecosystem demonstrate low winter growth and variable size-structured survival", I demonstrate the use of finite mixture distribution models to classify recruitment pulses in age-0 and age-1 Atlantic cod for the 2018 cohort. I then use insights gained during the development of these models to examine pulse structure across a 23-year time series to evaluate changes in winter growth and mortality across intra-annual pulses and annual cohorts.

In Chapter 4 "Condition, size, and winter duration affect winter survival probability in juvenile Atlantic cod (*Gadus morhua*) in a coastal subarctic ecosystem" (*in review,* Marine Ecology Progress Series), I examine relative winter survival of multiple age-0 Atlantic cod settlement pulses in relation to winter duration, body condition, and settlement time.

In Chapter 5 "Food and initial size influence overwinter survival and condition of a juvenile marine fish (age-0 Atlantic cod)" (published, Canadian Journal of Fisheries Aquatic Sciences, 2021), I use an experimental approach to assess the role of food and body size on overwinter condition, growth, and survival in age-0 Atlantic cod.

Lastly, in Chapter 6 “High site-fidelity and low mortality of juvenile Atlantic cod (*Gadus morhua*) in sub-arctic coastal habitat during their first winter” (published, ICES Journal of Marine Science, 2022), I apply capture-mark-recapture techniques to evaluate overwinter survival and site fidelity of three age-0 cod recruitment pulses.

Combining the three different forms of inference I have used in my dissertation (modeling, laboratory, field) provides access to knowledge typically unavailable in most studies. Limitations to winter studies include challenges in winter sampling, restricted explanatory variables within experimental studies, and lack of long-term datasets and individual inferences, limiting our capacity to answer critical scientific questions. Laboratory studies, for example, cannot address important questions regarding habitat use and mortality under natural conditions. Field studies cannot fully replicate the controlled environment of laboratory experiments, largely because external factors (e.g.., food availability, predation, weather events) add sources of variation. Likewise, natural seasonal variation and logistics limit the duration of field studies. High annual variation in long-term data adds noise and challenge to statistical models. However, long-term modelling studies evaluate trends shown in the wild that laboratory and field results can subsequently validate. Understanding overwinter dynamics in age-0 marine fish can help in predicting recruitment at an earlier stage and inform management decisions to protect northern fish populations. This research contributes significantly to early life history research in marine fishes and to fish ecology more generally. My research contributes substantive knowledge to support fisheries management in Newfoundland, but also applies more broadly to management of north temperate and subarctic species elsewhere.

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Chapter 2 – Natural mortality rates of fishes in the ocean: a review across multiple life stages

2.1 Abstract

Mortality rates play an important, yet poorly understood role in population dynamics. Understanding population growth or decline requires knowledge of mortality rates. However, quantification of mortality rates in marine populations is notoriously difficult, especially in fishes. The many distinct challenges (e.g., sampling, stochastic variation) have led to assumptions of constant natural mortality within a given life stage. I review approaches to estimating natural mortality, with a specific focus on life history traits for egg, larval, juvenile, and adult marine fish. In the second part of this chapter, I compare natural mortality rates for each of these life history stages. I use generalized linear models to compare natural mortality rates between taxonomic orders and regions within each life stage. I also review age and size as an estimator for adult natural mortality rates. Results highlight large variability among species and geographic regions, but age and size were strong predictors of natural mortality in older adult fish. The inherent variability in natural mortality rates across life stages compared in this review further supports non-constant, natural variation.

2.2 Introduction

Understanding population growth in any given species requires knowledge of mortality rates through its life stages. Thus, the difficulty and need to estimate mortality rates in marine fish populations has gained recent attention (Then *et al.*, 2015; Dureuil *et al.*, 2021; Punt *et al.*, 2021). Interconnected, three-dimensional oceans provide various habitat seascapes where life history strategies and stages influence species distributions, noting the tendency of fish populations to encompass large numbers of subpopulations, span large geographic scales, and naturally fluctuate in population size (Hjort, 1914, 1926).

In marine systems, ecologists often divide mortality into two components: fishing mortality and natural mortality. Fishing mortality represents the proportion of fish taken from the ocean through fishing activities, whereas natural mortality encompasses all other mortality not associated with fishing. Many studies attribute most natural mortality to predation, but others emphasize starvation (Sogard, 1997; Jørgensen *et al.*, 2016) and poor condition (Dutil and Lambert, 2011; Regular *et al.*, 2022) or disease (Vetter, 1988). Age, size, growth, and density also contribute to predation loss (Werner and Gilliam, 1984; McGurk, 1986; Anderson, 1988; Bailey and Houde, 1989), whereas food availability and temperature can cause starvation (Vetter, 1988; Sewall *et al.*, 2019).

Despite its importance for fisheries management, estimating natural mortality remains challenging (DFO, 2019; Rose and Walters, 2019) due to temporal variability, change in climate, and difficulty incorporating multiple life stages. In this chapter I: 1) review approaches to determining natural mortality rates from egg, larval, juvenile, and adult stages, and 2) compare natural mortality rates among various species within egg, larval, juvenile, and adult stages. The overall objective of this chapter is to review natural mortality rates and highlight the inherent variability between and within life stages.

2.3 Approaches to estimating natural mortality

Approaches to natural mortality estimates include catch-curve analyses (Edser, 1908; Ricker, 1975; Quinn and Deriso, 1999), linear regression with abundance estimates (Gulland, 1983; Beverton and Holt, 1993), or capture-mark-recapture techniques (Jackson, 1939; Lindberg, 2012). These methods rely on consistent population monitoring or unexploited populations. Determining natural mortality can be particularly challenging for exploited populations or situations with limited data. Determining the relationship between life history traits and natural mortality rates offers one solution. Traits such as age (Cushing, 1975; Hoenig, 1983), size (Blaxter and Hempel, 1963; Fenchel, 1974; Peterson and Wroblewski, 1984; Beverton and Holt, 1993; Lorenzen, 1996), growth (Ware, 1975; Silvert and Platt, 1978; Pauly, 1980), metabolic capacity (Ursin, 1967; Peters, 1983), and fecundity (Cushing, 1971) all provide potential indicators of natural mortality. Life history strategies encompass maintenance, growth, and reproduction, with trade-offs determining allocation of time and energy for each component (Gadgil and Bossert, 1970). Although some researchers treat life history traits such as growth, maximum size, and aging as invariant (Charnov, 1993), environmental and human impacts in marine systems can alter invariant traits (Anthony and Fogarty, 1985; Gårdmark *et al.*, 2003; Jørgensen and Fiksen, 2010; Enberg *et al.*, 2012).

2.3.1 Natural mortality in the egg and larval stage

Optimal egg size reflects a balance between weight and abundance to ensure that eggs survive to the larval stage with sufficient numbers and energy stores to survive until larvae locate food (Ware, 1975). Egg size can strongly influence growth rate and length during the larval stage. *Clupea harengus* larvae from large eggs lived for about 28 days with no food after hatching at 8 °C, whereas larvae from small eggs lived for 15 days in the same conditions (Blaxter and Hempel, 1963). Despite the importance of egg size for the survival of subsequent life stages, mortality during the egg stage is independent of size (Blaxter and Hempel, 1963; Pepin, 1991).

Many studies consider the larval stage as the determining period of year-class strength (Bannister *et al.*, 1974), an idea first hypothesized by Hjort (1914). Hjort noticed that abundance of fish decreased immediately following yolk-sac was absorption, and larvae began to actively seek food. The "critical period", referring to the period when complete yolk absorption occurs and high mortality ensues, was first applied by French fish culturists (Fabre-Domergue and Biétrix, 1897 as cited in May, 1974), but the difficulty in interpreting larval survival curves complicates confirmation or rejection of the critical period hypothesis (May, 1974). Density of larvae, density and size of prey, patchiness of plankton distribution, population dynamics of the prey, consumption rates, search and travel time, and dispersion and migration of larvae in relation to plankton can all contribute to larval starvation (Hempel, 1962).

The "match-mismatch" hypothesis (Cushing, 1990) also addresses larval mortality and food availability by considering the timing of plankton blooms in relation to fish spawning times. The match-mismatch hypothesis predicts release of eggs by fish so that larval hatch coincides with peaks in plankton production. It also predicts variation in larval growth rate from year to year based on food availability, with the earliest link between recruitment and food observed during the larval period (Cushing, 1990). Match-mismatch dynamics have been shown in Northeast Arctic cod (*Gadus morhua*; Ferreira *et al.*, 2020; Endo *et al.*, 2022) and Alaskan Pacific cod (*Gadus macrocephalus*; Laurel *et al.*, 2021). Match-mismatch dynamics can be caused by spatial and temporal overlaps between larvae and prey (Ferreira *et al.*, 2020) and strongly associated with temperature (Laurel *et al.*, 2021; Endo *et al.*, 2022).

Growth rate also influences mortality rates in larval fish. Pepin (1991) reviewed mortality in pelagic larval fishes and found a strong relationship between daily mortality rates of larvae and growth rates. High mortality rates characterized species with high growth rates, but mortality decreased as size increased in all taxa (Miller *et al.*, 1988). Temperature also significantly influenced daily development and mortality rates, with an increase in temperature leading to more rapid development in early life stages (Pepin, 1991). Additionally, McGurk (1986) reviewed natural mortality rates of marine pelagic larvae and found that spatial patchiness was directly proportional to natural mortality rates.

2.3.2 Natural mortality in the juvenile stage

The juvenile stage is a critical transition from the larval stage. Juveniles often change habitats and shift food sources (Grant and Brown, 1998; Ottersen *et al.*, 2014). Additionally, fishes transition from assumed density independent effects in the egg and larval stages (Myers, 2001) to density dependent effects during the juvenile stage (Myers and Cadigan, 1993). Juvenile natural mortality is largely attributed to predation (Sogard, 1997; Van der Veer *et al.*, 1997). In coral reef habitats, predators consume ~56% of juvenile fishes within the first few days of settlement (Almany and Webster, 2006). Predation levels vary depending on size, growth, and predator evasion.

Size and growth play an important role in susceptibility to predation. Predation rates can be influenced by predator to prey size ratio; small predators have a larger ratio (i.e., consume smaller prey) relative to large predators (Dörner *et al.*, 2007) and are often constrained by morphology, such as gape size (Schmitt and Holbrook, 1984). It is unclear if faster growth reduces predation risk. In theory, increased growth reduces time spent in a vulnerable size-class, and should minimize predation risk (Werner and Gilliam, 1984). However, predation risk increased for rainbow trout (*Oncorhynchus mykiss*) when growth rates were higher (Biro *et al.*, 2004). Behavioural trade-offs between growth and mortality indicate that age-0 rainbow trout select against high growth to avoid predators (adult trout; common loons, *Gavia immer*; Biro *et al.*, 2006).

Nursey habitats are important for juvenile fishes (Rauck and Zijlstra, 1978; Gotceitas *et al.*, 1997; Beck *et al.*, 2001), and provide important refuge from predators (Lindholm *et al.*, 1999; Lundvall *et al.*, 1999). Complex nursery areas can reduce predation risk for juvenile fish based on fragmentation (Laurel *et al.*, 2003), patch size and edges (Gorman *et al.*, 2009), and overall cover from predators (MacRobert, 2020). Kelp perch (*Brachyistius frenatus*), temperate reef fish, experience lower predation rates when they have access to structurally complex habitat, but the effect of habitat refuge is reduced when kelp perch have high abundance, indicating density-dependent mortality (Anderson, 2001).

Juvenile fish are also susceptible to predators based on levels of available energy storage (Mogensen and Post, 2012). Fishes with high energy reserves can avoid high-risk foraging behaviours that reduce predation (Biro *et al.*, 2005; Sewall *et al.*, 2019). For example, age-0 rainbow trout allocate energy to somatic growth during low-food periods (high risk habitats) and switch to lipid allocation during high-food periods (low risk habitats; Biro *et al.*, 2005). Juvenile Atlantic herring (*Clupea harengus*) show similar trends, and shift from protein-based growth to lipid storage when they reach a certain length before their first winter (Sewall *et al.*, 2019). Juvenile natural mortality is therefore dynamic due to interactions between predators, foraging, and habitat use.

2.3.3 Natural mortality in the adult stage

Size-structure of fish populations link to population dynamics and enable determination of natural mortality rates (Fenchel, 1974; Blueweiss *et al.*, 1978; Werner and Gilliam, 1984). As fish grow and become larger, their susceptibility to predation decreases (Werner and Gilliam, 1984). Previous work has estimated size-dependent mortality rate for juvenile and adult pelagic fish using a weight exponent for growth and metabolic rate (Peterson and Wroblewski, 1984).

Multiple studies confirm the relationship between size and natural mortality (Pauly, 1980; McGurk, 1986; McGurk, 1987; Griffiths and Harrod, 2007). However, researchers have proposed different relationships between weight and natural mortality rate (Gulland, 1987; Lorenzen, 1996; Gislason *et al.*, 2010), including weight exponents for mortality ranging from 0.25 (Peterson and Wroblewski, 1984) to 1.6 (Gislason *et al.*, 2010). Lorenzen (1996) calculated a weight exponent of 0.37 for all life stages of fishes, which reflects weight exponents of 0.34 for juvenile and adult fishes, and 0.49 for eggs and larvae. Importantly, the differences in parameter estimates highlight the variability in mortality. Lorenzen's (1996) study incorporated fishes from diverse habitats (lakes, rivers, and oceans) and regions (tropical, temperate, and polar) and found a similar relationship between natural mortality and body weight across all systems. However, many studies show that body mass and size do not explain all variation in natural mortality. For example, Griffiths and Harrod (2007) reported that phylogenetic and behavioral traits influence natural mortality rates in fishes.

North Sea fish communities demonstrate both size- and habitat-dependent natural mortality, with differing mortality rates between demersal and pelagic stages (Gislason *et al.*, 2008). Pauly (1980) reviewed natural mortality rates from 175 fish stocks and assessed the effect of size, growth, and temperature on rates, and confirmed the link between natural mortality rate, size, and growth efficiency rate. Natural mortality also correlated with environmental temperature but was unimportant as a predictive factor when growth efficiency rate was available (Pauly, 1980). Reanalysis of the same data on 175 stocks using principal component analysis separated mortality rates into two groups: temperate waters and warmer waters (Jensen, 2001). The variety of explanatory variables illustrates that a single life-history trait cannot explain natural mortality across fish species.

Assessments of adult populations often assume constant and stable natural mortality throughout the adult stage. Maximum age of the species/population offers a common metric to assess natural mortality in adult stages in the absence of direct approaches (catch-curve analyses, tagging studies, Bayliff, 1967; Hoenig, 1983). Recent reviews confirm age as a preferable explanatory variable to temperature, size, and growth parameters (Then *et al.*, 2015; Dureuil *et al.*, 2021). However, a limitation of using age is it can only be used to determine total mortality Z and requires a reliable estimate of maximum age achievable within populations (Kenchington, 2014). Hoenig's and Pauly's estimators applied to scarlet sea perch (*Lutjanus malabaricus*) showed that the former provided results similar to catch-curve analyses of scarlet sea perch natural mortality, whereas the latter overestimated natural mortality rate, thus underestimating survivorship (Newman, 2002). Another case study reported biases in natural mortality rate estimates from age-variation that were secondary to temporal trends, such as annual fluctuations (Deroba and Schueller, 2013). These studies further highlight that natural mortality is not constant and no single metric can reliably predict natural mortality on an annual basis.

2.4 Comparison of natural mortality rates

2.4.1 Data sources and statistical analyses

In order to compare natural mortality rates, I collected natural mortality rates (M) for egg ($M \cdot d^{-1}$), larval ($M \cdot d^{-1}$), juvenile ($M \cdot d^{-1}$), and adult ($M \cdot y^{-1}$) stages from 50 studies and 35 species, along with additional adult stage mortality rates (n = 172) from the Virginia Institute of Marine Science (VIMS) College of William and Mary database (Then and Hoenig, 2015). I only included analysis of natural mortality rates that were not part of the VIMS database if I could verify them in original publications. I then compared natural mortality rates (mean ± s.d.) among taxonomic orders, regions, and habitats for egg mortality rates using a generalized linear model with a gamma distribution and log link. Comparisons of taxonomic order and region for larval and adult mortality rates used the same error distribution and link function, noting separate analyses for explanatory variables (taxonomic order, region, habitat). In cases of statistically significant explanatory variables ($p < 0.05$), I used Akaike Information Criteria (AIC) to determine which model accounted for the most explained variance in natural mortality rates. Comparison of juvenile natural mortality rates was not possible due to limited sample size, with only 4 species available. Annual instantaneous mortality rates ($M \cdot y^{-1}$) were reviewed for adult stage. Comparisons of adult natural mortality rates in relation to maximum size ($L\infty$) and maximum age used a generalized linear model with a gamma distribution and log link.

2.4.2 Egg stage

My literature survey of 11 different studies yielded 56 natural mortality rates for the egg stage of 8 species (Appendix 2.1). Atlantic cod (*Gadus morhua*), haddock, (*Melanogrammus aeglefinus*), and European plaice (*Pleuronectes platessa*) yielded a similar natural morality rate, $M \cdot d^{-1}$, (0.11 ± 0.02, 0.08 ± 0.02, and 0.08 ± 0.01, respectively). Highest natural mortality rate estimates were reported for South American pilchard (*Sardinops sagax*), Peruvian anchovy (*Engraulis ringens*), and Argentine anchovy (*E. anchoita*), with South American pilchard at 1.73 ± 0.75 d^{-1}, Peruvian anchovy at 1.32 ± 0.41 d^{-1}, and Argentine anchovy at 0.90 d^{-1}.

The respective models for taxonomic orders and regions all indicated statistically significant differences, with region accounting for the most explained variance (Table 2.1). Clupeiformes from tropical waters numbered among the highest natural mortality values. Lastly, eggs in coastal habitats had a higher natural mortality rate relative to pelagic and benthopelagic eggs (Fig. 2.1).

Table 2.1. Analysis of Deviance (ANODEV) and Akaike Information Criteria (AIC) scores for three models with a Gamma distribution: Egg natural mortality (response) and the following three explanatory variables: Taxonomic order, region, and habitat. ANODEV variables include Likelihood ratio Chi-square (LR Chisq), degrees of freedom of parameters (Parameter DF), and p-value (p); degrees of freedom for the model (Model DF) are included with AIC. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.1.

Parameter	LR Chisq	Parameter DF	p	Model DF	AIC
Order	75.10	3	$3.4 \cdot 10^{-16}$	5	-66.13
Region	100.8	3	$<2.2 \cdot 10^{-16}$	5	-71.34
Habitat	45.77	2	$1.2 \cdot 10^{-10}$	4	-55.41

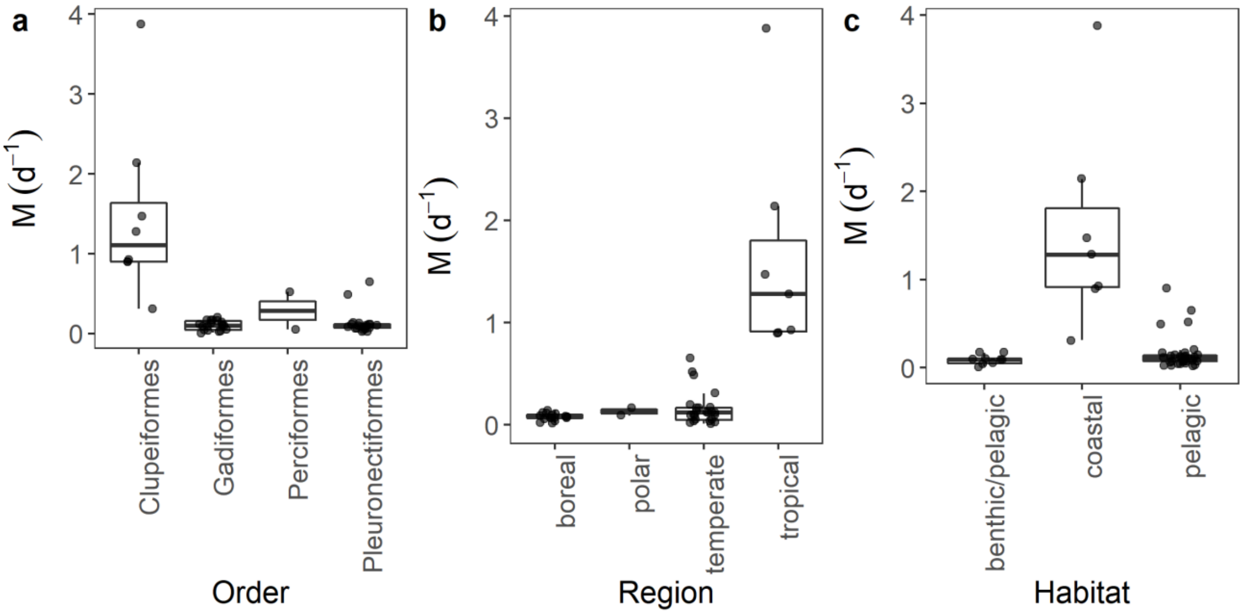

Figure 2.1. Daily instantaneous natural mortality rate ($M \cdot d^{-1}$) in eggs by a) Taxonomic order, b) region, and c) habitat. The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Points represent individual mortality rates. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.1.

2.4.3 Larval stage

Collection of information from larval stages of 11 species from 17 different studies yielded 52 natural mortality rates (Appendix 2.2). Lowest mean mortality rates occur in Atlantic herring (*Clupea harengus*), European plaice, and redfish (*Sebastes* spp.), with a rate of 0.05 ± 0.02 in Atlantic herring and European plaice, and a rate of 0.06 ± 0.01 d^{-1} in redfish.

Taxonomic order and region were both statistically significant in their respective models, with order accounting for the most explained variance among natural mortality values (Table 2.2). *Perciformes* had the highest natural mortality rate (Fig. 2.2a). Despite a higher natural mortality rate for subtropical regions than the other two regions, higher variation characterized the temperate region, possibly reflecting a larger sample size (Fig. 2.2b).

Table 2.2. Analysis of Deviance (ANODEV) and Akaike Information Criteria (AIC) scores for two models with a Gamma distribution: Larval natural mortality (response) and the following two explanatory variables: Taxonomic order and region. ANODEV variables include Likelihood ratio Chi-square (LR Chisq), degrees of freedom of parameters (Parameter DF), and p-value (p); degrees of freedom for the model (Model DF) are included with AIC. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.2.

Parameter	**LR Chisq**	**Parameter DF**	**p**	**Model DF**	**AIC**
Order	30.15	4	$4.6 \cdot 10^{-06}$	6	-129.4
Region	17.14	2	0.00019	4	-124.2

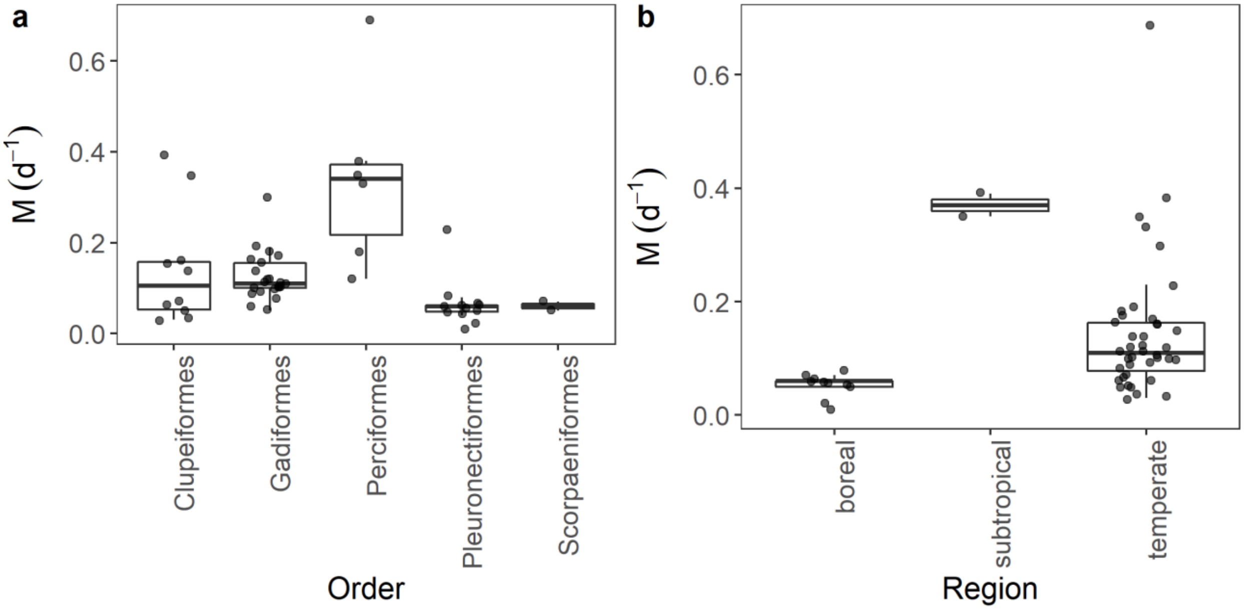

Figure 2.2. Daily instantaneous natural mortality rate (M·d^{-1}) in larval fish by a) Taxonomic order and b) region. The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Points represent individual mortality rates. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.2.

2.4.4 Juvenile stage

Juvenile natural mortality rates were limited within literature and resulted in 19 rates of 4 species (*Gadus morhua, G. macrocephalus ogac, Pseudopleuronectes americanus, Pleuronectes platessa*) from 7 studies (Appendix 2.3). Lowest mortality rate occurred in age-1 Atlantic cod (*G. morhua*; M=0.00014) and highest mortality rate occurred in age-0 European plaice (*P. platessa*; M=0.0926). Age-0 natural mortality rates ranged from 0.0047 – 0.0926, and age-1 natural mortality rates ranged from 0.0014 – 0.068 (Fig. 2.3).

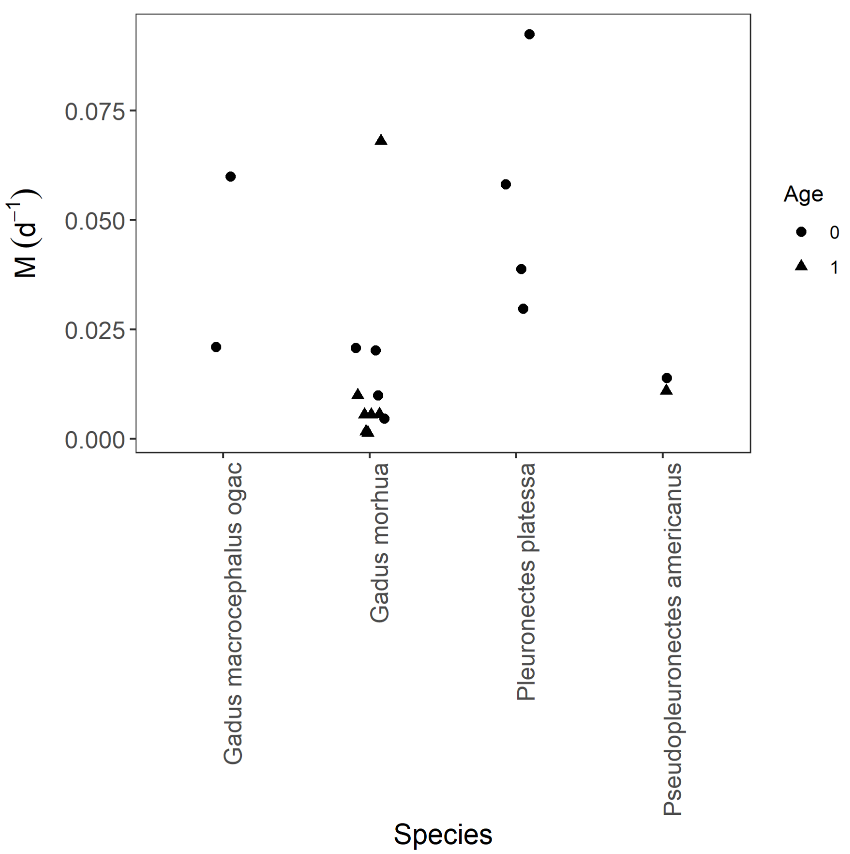

Figure 2.3. Daily instantaneous natural mortality rate (M·d^{-1}) in juvenile fish by species. Points represent individual mortality rates. Circles represent age-0 juveniles and triangles represent age-1 juveniles. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.3.

2.4.5 Adult stage

A total of 21 species collected from 19 studies yielded 48 adult natural mortality rates (Appendix 2.4). The VIMS database contributed another 185 adult natural mortality rates. Adult mortality rates ranged from 0.01 to 7.9 y^{-1}. I limited analyses comparing taxonomic orders and geographic regions to those orders represented by 3 or more mortality estimates. Order and region models both yielded statistically significant differences, with order accounting for the most explained variance among natural mortality values (Table 2.3). When separated by order, Myctophiformes (lanternfish) yielded the highest mean natural mortality rate (M=0.98 ± 0.42 y^{-1}), with the lowest mean mortality rate (M = 0.10 ± 0.07) in subclass Elasmobranchi. Perciformes had the largest variance, ranging from M = 0.01 y^{-1} (*Pomatoschistus minutus*) to M = 7.92 y^{-1} (*Istigobius decorates*). The differences among regions were small, with the highest range within the subtropical (0.02 – 5.07 y^{-1}) and tropical populations (0.08 – 7.92 y^{-1}; Fig. 2.4).

Table 2.3. Analysis of Deviance (ANODEV) and Akaike Information Criteria (AIC) scores for two models with a Gamma distribution: Adult natural mortality (response) and the following two explanatory variables: Taxonomic order and region. ANODEV variables include Likelihood ratio Chi-square (LR Chisq), degrees of freedom of parameters (Parameter DF), and p-value (p); degrees of freedom for the model (Model DF) are included with AIC. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.4.

Parameter	LR Chisq	Parameter DF	p	Model DF	AIC
Order	22.0	8	0.0049	10	161.7
Region	9.57	4	0.048	6	178.7

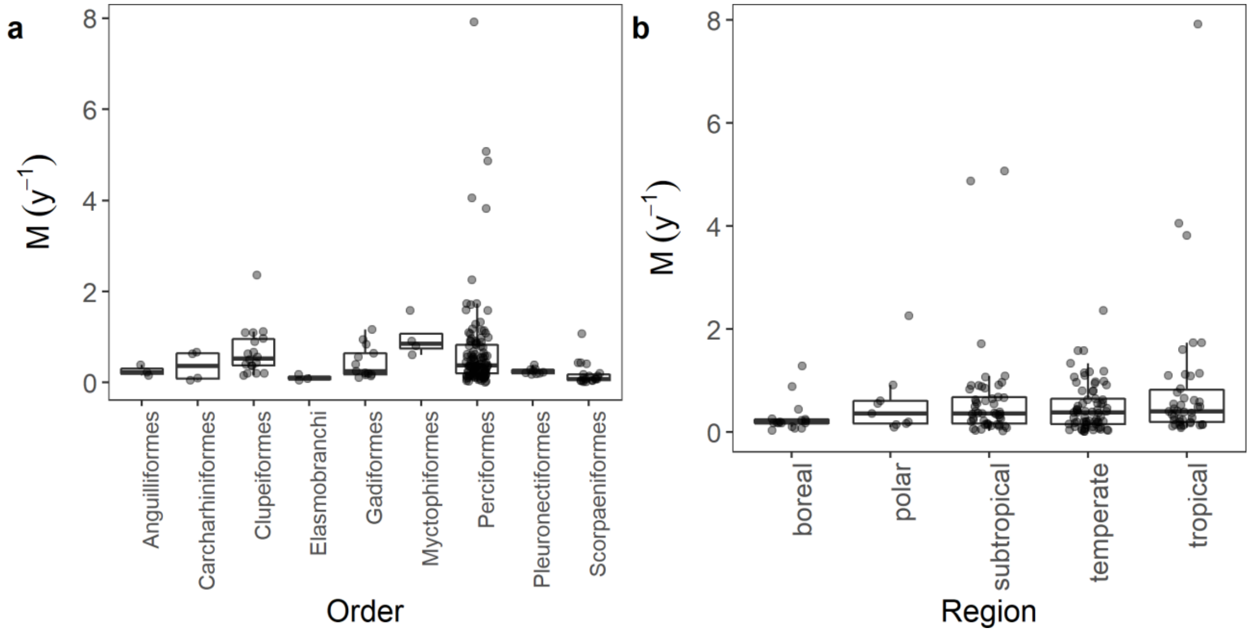

Figure 2.4. Annual instantaneous natural mortality rate ($M \cdot y^{-1}$) in adult fish by a) Taxonomic order and b) region. The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Points represent individual mortality rates. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.4.

Maximum age and maximum length both explained significant variation in adult natural mortality rate when included in models separately (Size: $\chi^2 = 22.90$, $p < 0.001$; Age: $\chi^2 = 173.56$, $p < 0.001$; Fig. 2.5). However, when including age and length in a model together, only age proved statistically significant in explaining variation in natural mortality (Table 2.4).

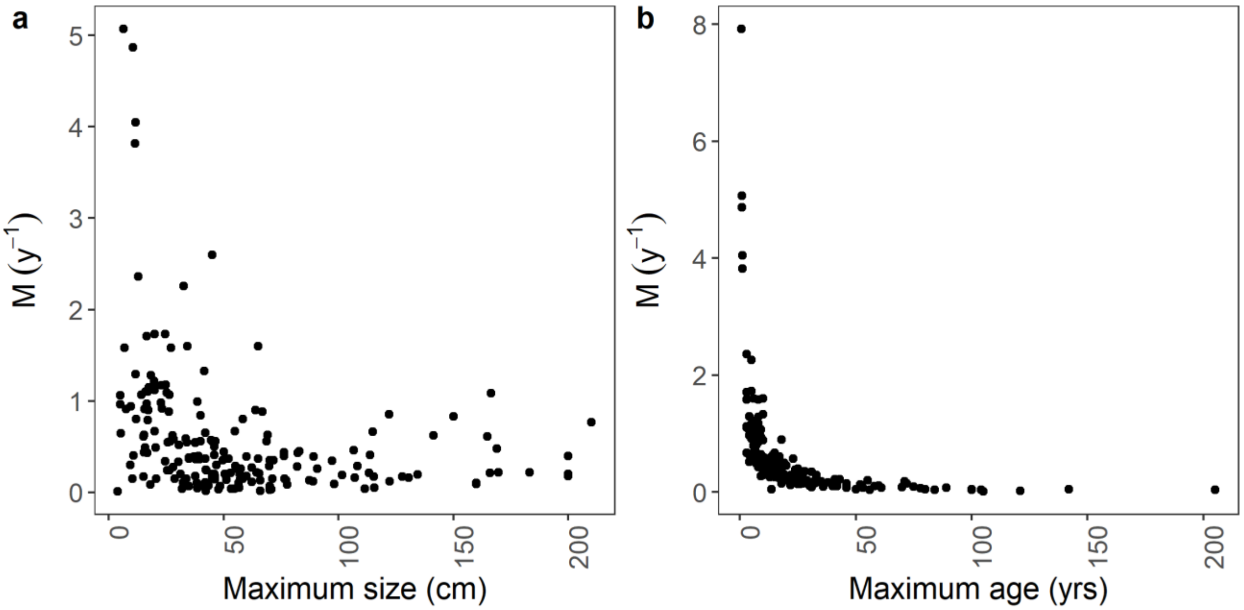

Figure 2.5. The relationship between a) maximum size (cm) and b) maximum age (yrs) and natural mortality rate ($M \cdot y^{-1}$) of adult fish. Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.4.

Table 2.4. Analysis of Deviance (ANODEV) of the effect of age and size on adult natural mortality. The interactive effect did not converge and was therefore removed from the model. Model was run using a Gamma distribution. ANODEV variables include Likelihood ratio Chi-square (LR Chisq), degrees of freedom of parameters (DF), and p-value (p). Data were collected from peer-reviewed publications and databases which can be referred to in Appendix 2.4.

Explanatory variable	**LR Chisq**	**DF**	**p**
Age	157.6	1	$<2.0 \cdot 10^{-16}$
Size	1.324	1	0.25

*interactive effect did not converge

2.5 Discussion

2.5.1 Mortality rate comparison

Region explained the most variance in natural mortality within the egg stage, with highest natural mortality in the tropical region. Timing of spawning and temperature influence how quickly eggs develop (Pauly and Pullin, 1988; Snelgrove *et al.*, 2008), with typically higher survivorship in eggs with shorter duration (Pepin *et al.*, 1997). Based on temperature alone, I expected low natural mortality rates in tropical regions. However, temperature by itself cannot explain variation in egg survival, and mortality rates in the egg stage vary among and within species because of the influence of density, patchiness, and predator distribution (Bailey and Houde, 1989).

Taxonomic order, rather than region, explained larval natural mortality rates best. Larval mortality links to multiple life history characteristics such as yolk sac absorption rate, growth (Pepin, 1991), size (Cowan *et al.*, 1996), and patchiness (Hewitt, 1981). The lowest natural mortality occurred in Scorpaeniformes, represented here by redfish (*Sebastes* spp.). Low natural mortality rates characterize redfish throughout their entire lifespan. Redfish are live-bearers with internal egg fertilization in which larval development occurs within the oviduct. Once released near the end of the yolk-sac phase, redfish larval duration lasts 3-4 months, during which newly spawned larvae live in the upper 10 m of the water column before migrating towards the thermocline at 10-25 mm in length (Pikanowski *et al.*, 1999). Highest larval natural mortality rate values were in Perciformes, represented by Atlantic mackerel (*Scomber scombrus*) and Pacific jack mackerel (*Trachurus symmetricus*), which grow to maximum larval lengths of 5 mm for Pacific jack mackerel in contrast to a settlement size in around 10 mm in length for Atlantic mackerel (MacGregor, 1966; Studholme *et al.*, 1999).

Taxonomic order and region influenced adult mortality rates less than egg and larval stage. However, age was an important explanatory variable for adult natural mortality rates (Hoenig, 1983; Then *et al.*, 2015). Constant natural mortality rate over time tends to characterize long-lived species compared with a survival curve with a downward curvature throughout most of the lifespan of short-lived species (Beverton and Holt, 1959). Although significant as an explanatory variable, size varied more than age. For example, the lowest mortality rate (M = 0.01) occurred in sand goby (*Pomatoschistus minutus*) from a temperate reef with a maximum size of 4.0 cm. In comparison, the next smallest fish in the dataset, the eastern mosquitofish (*Gambusia holbrooki*) at 4.85 cm and an M = 2.72, occurs in subtropical regions. In contrast, size can be an important predictor within families, such as skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tuna, which exhibit strong size-specific mortality rates (Hampton, 2011). Noting temperature impacts, using size as an indicator of mortality might benefit from restricting observations to those within specific geographic regions (Pauly, 1980).

There are a limited number of publications that estimate daily instantaneous natural mortality rate during the juvenile stage. Based on high variability seen in the egg and larval stage, juvenile fishes are likely to show high variation between regions and species. The juvenile stage is an important link between larval and adult stages, and natural mortality rates of juveniles should be further investigated across multiple systems. The juvenile stage provides additional challenges given the wide age range (0-3) and transition in life history strategies exhibited within this life phase, itself. Fish experience variable growth rates throughout the juvenile stage. Additionally, juvenile fish often experience diet (Dalpadado and Bogstad, 2004) and habitat (Elliott *et al.*, 2017) shifts, which contrast egg, larval, and adult stages.

Incorrect assessment of natural mortality rates can have serious implications for management decisions (Kenchington, 2014; Punt *et al.*, 2021). Comparing natural mortality rates further highlights the high variability of natural mortality rate within and across life stages. Life history strategies can help explain some variation but increased research on explanatory factors beyond life history strategies (e.g., predation and food availability) across regions, species, and life stages is necessary to produce better natural mortality estimates.

2.5.2 Variability in estimating natural mortality rates

Regardless of the inherent variability in natural mortality, stock assessments based upon mature individuals of a population still consider constant natural mortality rates as appropriate (Dureuil *et al.*, 2021). Previous analyses all evaluated natural mortality rate as a constant value, known as the “constant M axiom” (Caddy, 1991). However, the variability reported here demonstrates the problem of assuming constant mortality rate. Through egg, larval, juvenile, and adult stages, fishes experience variable mortality rates described by multiple rather than a single survival curve (Deevey, 1947; Pinder *et al.*, 1978). For example, natural variation in mortality rates in early and late larval stages largely influences population growth in northern anchovy (*E. mordax*). The natural variation during these stages was largely attributed to changes in stage duration (Butler *et al.*, 1993). Marine organisms experience external factors such as temperature, predator abundance, density, and food supply (Vetter, 1988), emphasizing the importance of incorporating variation when estimating natural mortality rates. Behavioural and life history strategies can shape these external factors and can result in selective natural mortality (Jørgensen and Holt, 2013; Johnson *et al.*, 2014). Natural variation in mortality rates can have important implications for management decisions (Punt *et al.*, 2021). Incorrectly specified natural mortality can result in large error in stock size estimates (Sims, 1984; Vetter, 1988; Clark, 1999) and can lead to unanticipated events like “recruitment failures”. Many parameters have unknown effects on abundance and natural mortality for which estimates of natural mortality must account. Understanding the drivers of growth and survival can improve understanding of fish populations and quantitative assessments should incorporate these variables (Pepin, 2016) once we can identify their effects under different climate scenarios. Recent studies have incorporated condition metrics to assess population recovery (Morgan *et al.*, 2018) and starvation-induced mortality in northern cod (Regular *et al.*, 2022). Additionally, assessments of population dynamics can account for species interactions, as well as their effects on natural mortality (Link *et al.*, 2011; Buren *et al.*, 2014a, 2014b; Koen-Alonso *et al.*, 2021).

Overlooking biological significance of factors and parameters can create additional challenges in estimating M with model-based approaches. Pauly (1980) related natural mortality to temperature, growth, length, and weight, but only temperature and growth were significant in the model, leading him to conclude that growth rate and temperature were better indicators of natural mortality rate than size. Jensen (2001) revaluated Pauly’s analysis and concluded that although Pauly’s model was useful for predictions, it did not correctly identify the relationship among the variables – as growth, temperature, and size all covary. When evaluated individually, all relationships between variables become significant. However, because temperature directly affects mortality rate and indirectly affects mortality rate through growth, the results of multiple linear regression differed from those based on simple linear regression (Jensen, 2001). The collinearity among the variables allows for development of a predictive model but constrains inferences on the relationship among variables (Jensen, 2001).

In conclusion, natural mortality rates are non-constant variables. Numerous studies have highlighted the inherent variability in natural mortality (Myers and Doyle, 1983; Myers, 2001;

Then *et al.*, 2015; Dureuil *et al.*, 2021), and recent literature emphasizes the importance of understanding mortality for research on population dynamics and management (Deroba and Schueller, 2013; Punt *et al.*, 2021). Rather than creating an obstacle, variability in natural mortality should be seen as an opportunity to advance understanding of population dynamics. Addressing the drivers that influence natural mortality and incorporating those mechanisms into ecological models offers one pathway to embrace variability in in natural mortality rates instead of setting them as fixed parameters. Each life stage faces a unique set of biotic and abiotic challenges; therefore, future work should consider natural mortality across multiple life stages (Ottersen *et al.*, 2014).

2.6 Acknowledgements

This chapter was developed from Memorial University School of Graduate Studies Comprehensive exam through the Biology Department. The exam question was initially developed by P.V.R. Snelgrove, R.S. Gregory, I.A. Fleming, and E. Vander Wal. This research was further sponsored by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada (including Productive Capacity and Marine Conservation Targets programs) and INREST (representing the Port of Sept-Îles and City of Sept-Îles, Quebec).

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2.8 Appendix

Appendix 2.1. Natural daily instantaneous mortality rates (M · d^{-1}) of marine fish during the egg stage.

Order	**Species**	**Common Name**	**M (d^{-1})**	**Region**	**Habitat**	**Source for M**	**Source for habitat**
Clupeiformes	*Engraulis anchoita*	Argentine anchovy	0.9	tropical	pelagic	Ciechomski and Capezzani, 1973	Ciechomski and Capezzani, 1973
Clupeiformes	*Engraulis ringens*	Peruvian anchovy	2.14	tropical	coastal	Smith *et al.*, 1989	Smith *et al.*, 1989
Clupeiformes	*Engraulis ringens*	Peruvian anchovy	0.93	tropical	coastal	Smith *et al.*, 1989	Smith *et al.*, 1989
Clupeiformes	*Engraulis ringens*	Peruvian anchovy	0.9	tropical	coastal	Smith *et al.*, 1989	Smith *et al.*, 1989
Clupeiformes	*Sardinops sagax*	South American pilchard	0.31	temperate		Smith, 1973	Smith, 1973
Clupeiformes	*Sardinops sagax*	South American pilchard	3.88	tropical	coastal	Smith *et al.*, 1989	Smith, 1973
Clupeiformes	*Sardinops sagax*	South American pilchard	1.28	tropical	coastal	Smith *et al.*, 1989	Smith, 1973
Clupeiformes	*Sardinops sagax*	South American pilchard	1.47	tropical	coastal	Smith *et al.*, 1989	Smith, 1973
Gadiformes	*Gadus morhua*	Atlantic cod	0.17	polar	pelagic	Langangen *et al.*, 2014	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.17	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.03	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.14	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.2	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999

Appendix 2.1 *continued*

Order	Species	Common Name	M (d^{-1})	Region	Habitat	Source for M	Source for habitat
Gadiformes	*Gadus morhua*	Atlantic cod	0.1	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.02	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.04	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.12	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.13	temperate	pelagic	Lough *et al.*, 2006	Fahay *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.09	polar	benthic/pelagic	Langangen *et al.*, 2014	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.1	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.17	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.09	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.17	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.1	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.04	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.05	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.01	temperate	benthic/pelagic	Lough *et al.*, 2006	Cargnelli *et al.*, 1999
Perciformes	*Scomber scombrus*	Atlantic mackerel	0.05	temperate	pelagic	Sette, 1943	Studholme *et al.*, 1999

Appendix 2.1 *continued*

Order	Species	Common Name	M (d-1)	Region	Habitat	Source for M	Source for habitat
Perciformes	*Scomber scombrus*	Atlantic mackerel	0.52	temperate	pelagic	Ware and Lambert, 1985)	Studholme *et al.*, 1999
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.07	boreal	pelagic	Bannister *et al.*, 1974	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.02	boreal	pelagic	Bannister *et al.*, 1974	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.07	boreal	pelagic	Bannister *et al.*, 1974	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.07	boreal	pelagic	Bannister *et al.*, 1974	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.12	boreal	pelagic	Bannister *et al.*, 1974	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.04	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.14	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.09	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.07	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.06	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.1	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.08	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.02	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.11	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974

Appendix 2.1 *continued*

Order	*Species*	Common Name	M (d-1)	Region	Habitat	Source for M	Source for habitat
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.08	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.12	boreal	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.13	temperate	pelagic	Harding *et al.*, 1978	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.12	temperate	pelagic	Nash, 1998	Bannister *et al.*, 1974
Pleuronectiformes	*Solea solea*	Common sole	0.49	temperate	pelagic	Riley, 1974	Koutsikopoulos and Lacroix, 1992
Pleuronectiformes	*Solea solea*	Common sole	0.65	temperate	pelagic	Riley, 1974	Bannister *et al.*, 1974

Appendix 2.2. Natural daily instantaneous mortality rates (M · d^{-1}) of marine fish during the larval stage.

Order	Species	Common Name	M (d^{-1})	Region	Source for M
Clupeiformes	*Clupea harengus*	Atlantic herring	0.06	temperate	Henderson *et al.*, 1984
Clupeiformes	*Clupea harengus*	Atlantic herring	0.07	temperate	Henderson *et al.*, 1984
Clupeiformes	*Clupea harengus*	Atlantic herring	0.03	temperate	Lough *et al.*, 1981
Clupeiformes	*Clupea harengus*	Atlantic herring	0.03	temperate	Lough *et al.*, 1981
Clupeiformes	*Clupea harengus*	Atlantic herring	0.05	temperate	Lough *et al.*, 1981
Clupeiformes	*Clupea pallasii*	Pacific herring	0.14	temperate	McGurk, 1986
Clupeiformes	*Engraulis mordax*	Californian anchovy	0.15	temperate	Hewitt and Methot, 1982
Clupeiformes	*Engraulis mordax*	Californian anchovy	0.16	temperate	Hewitt, 1981

Appendix 2.2 *continued*

Order	Species	Common Name	M (d^{-1})	Region	Source for M
Clupeiformes	*Opisthonema oglinum*	Atlantic thread herring	0.35	subtropical	Houde, 1977
Clupeiformes	*Opisthonema oglinum*	Atlantic thread herring	0.39	subtropical	Houde, 1977
Gadiformes	*Gadus morhua*	Atlantic cod	0.09	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.16	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.06	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.12	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.05	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.16	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.1	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.1	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.08	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.1	temperate	Lough *et al.*, 2006
Gadiformes	*Gadus morhua*	Atlantic cod	0.1	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.1	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.3	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.14	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.12	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.11	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.18	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.19	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.17	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.09	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.11	temperate	Lough *et al.*, 2006
Gadiformes	*Melanogrammus aeglefinus*	Haddock	0.11	temperate	Lough *et al.*, 2006
Perciformes	*Scomber scombrus*	Atlantic mackerel	0.35	temperate	Kendall and Gordon, 1981
Perciformes	*Scomber scombrus*	Atlantic mackerel	0.12	temperate	Sette, 1943

Appendix 2.2 *continued*

Order	***Species***	**Common Name**	**M (d-1)**	**Region**	**Source for M**
Perciformes	*Scomber scombrus*	Atlantic mackerel	0.38	temperate	Ware and Lambert, 1985
Perciformes	*Scomber scombrus*	Atlantic mackerel	0.69	temperate	Ware and Lambert, 1985
Perciformes	*Trachurus symmetricus*	Pacific jack mackerel	0.18	temperate	Hewitt, 1981
Perciformes	*Trachurus symmetricus*	Pacific jack mackerel	0.33	temperate	Hewitt *et al.*, 1985
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.06	boreal	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.06	boreal	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.01	boreal	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.06	boreal	Bannister *et al.*, 1974
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.08	boreal	Harding *et al.*, 1978
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.06	boreal	Harding *et al.*, 1978
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.02	boreal	Harding *et al.*, 1978
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.05	boreal	Harding *et al.*, 1978
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.07	temperate	Harding *et al.*, 1978
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.05	temperate	Nash, 1998
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.04	temperate	van der Veer, 1986
Pleuronectiformes	*Pseudopleuronectes americanus*	Winter flounder	0.23	temperate	Pearcy, 1976
Scorpaeniformes	*Sebastes* spp.	Redfish	0.05	boreal	Anderson, 1984
Scorpaeniformes	*Sebastes* spp.	Redfish	0.07	boreal	Anderson, 1984

Appendix 2.3 Natural daily instantaneous mortality rates (M · d^{-1}) of marine fish during the juvenile stage (age-0 and age-1).

Order	**Species**	**Common Name**	**M (d^{-1})**	**Age**	**Source for M**
Gadiformes	*Gadus macrocephalus ogac*	Greenland cod	0.06	0	Sheppard, 2005
Gadiformes	*Gadus macrocephalus ogac*	Greenland cod	0.021	0	Sheppard, 2005
Gadiformes	*Gadus morhua*	Atlantic cod	0.01	0	Julliard *et al.*, 2001
Gadiformes	*Gadus morhua*	Arctic cod	0.0203	0	Bogstad *et al.*, 2016
Gadiformes	*Gadus morhua*	Arctic cod	0.0209	0	Bogstad *et al.*, 2016
Gadiformes	*Gadus morhua*	Arctic cod	0.0047	0	Bogstad *et al.*, 2016
Gadiformes	*Gadus morhua*	Atlantic cod	0.01	1	Sheppard, 2005
Gadiformes	*Gadus morhua*	Atlantic cod	0.068	1	Sheppard, 2005
Gadiformes	*Gadus morhua*	Atlantic cod	0.0056	1	Kristiansen *et al.*, 2000
Gadiformes	*Gadus morhua*	Atlantic cod	0.0014	1	Julliard *et al.*, 2001
Gadiformes	*Gadus morhua*	Atlantic cod	0.0056	1	Ottera *et al.*, 1999
Gadiformes	*Gadus morhua*	Atlantic cod	0.0057	1	Ottera *et al.*, 1999
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.0926	0	Geffen *et al.*, 2011
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.0389	0	Geffen *et al.*, 2011
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.0583	0	Geffen *et al.*, 2011
Pleuronectiformes	*Pleuronectes platessa*	European plaice	0.0298	0	Geffen *et al.*, 2011
Pleuronectiformes	*Pseudopleuronectes americanus*	winter flounder	0.014	0	Tyler *et al.*, 1997
Pleuronectiformes	*Pseudopleuronectes americanus*	winter flounder	0.011	1	Tyler *et al.*, 1997

Appendix 2.4 Natural annual instantaneous mortality rates (M · y^{-1}) of adult marine fish.

Order	Species	Common Name	M (y^{-1})	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Acipenseriformes	*Acipenser transmontanus*	white sturgeon	0.18	316.4	71	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Anguilliformes	*Anguilla anguilla*	European eel	0.23		19	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Anguilliformes	*Anguilla japonica*	Japanese eel	0.39	89.12	10	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Anguilliformes	*Anguilla rostrata*	American eel	0.16		38	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Atheriniformes	*Atherina boyeri*	sand smelt	1.29	11.697	4	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Beloniformes	*Cololabis saira*	Pacific saury	1.6	34.236	6	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Beloniformes	*Hyporhamphus melanochir*	garfish	0.55	37.7	10	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Beryciformes	*Beryx splendens*	alfonsino	0.57	44.7	23	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Carcharhiniformes	*Carcharhinus sorrah*	spottail shark	0.05	115.55	13.7	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Carcharhiniformes	*Galeorhinus galeus*	school shark	0.1006	160	40	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Carcharhiniformes	*Rhizoprionodon taylori*	Australian sharpnose shark	0.63	69.235	7	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Carcharhiniformes	*Sphyrna tiburo*	bonnethead shark	0.6615	115	7	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Clupea harengus*	Atlantic herring	0.16	45	25	temperate	Beverton, 1963	Froese and Pauly, 2022
Clupeiformes	*Clupea harengus*	Atlantic herring	0.2	45	25	boreal	Beverton, 1963	Froese and Pauly, 2022
Clupeiformes	*Clupea harengus*	Atlantic herring	0.2	45	25	temperate	Beverton, 1963	Froese and Pauly, 2022
Clupeiformes	*Clupea pallasii*	Pacific herring	0.2	46	19	temperate	Beverton, 1963	Froese and Pauly, 2022

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Clupeiformes	*Clupea pallasii*	Pacific herring	0.5	46	19	temperate	Beverton, 1963	Froese and Pauly, 2022
Clupeiformes	*Sardinella longiceps*	Indian oil sardine	0.67	20	3	subtropical	Banerji, 1973	Froese and Pauly, 2022
Clupeiformes	*Sardinella longiceps*	Indian oil sardine	1.12	20	3	tropical	Sekharan, 1975	Froese and Pauly, 2022
Clupeiformes	*Sardinops sagax*	South American pilchard	0.4	39	25	temperate	Beverton, 1963	Froese and Pauly, 2022
Clupeiformes	*Anchoa mitchilli*	bay anchovy	2.36	12.93	3	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Brevoortia patronus*	Gulf menhaden	1.09	25.27	4	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Brevoortia tyrannus*	Atlantic menhaden	0.37	34.97	10	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Clupea pallasii*	Pacific herring	0.56	27	11	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Engraulis anchoita*	Argentine anchovy	0.9	17.3	8	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Engraulis japonicas*	Japanese anchovy	0.63	15.5	4	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Engraulis mordax*	northern anchovy	0.97	16.552	7	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Engraulis ringens*	Peruvian anchoveta	1.1	16.98	3	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Sardinops sagax*	pilchard, Pacific sardine	0.43	16.8	8	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Clupeiformes	*Sardinops sagax*	South American pilchard	0.38	39		temperate	Clark and Marr, 1955	Froese and Pauly, 2022
Elasmobranchi	*Cetorhinus maximus*	Basking shark	0.05	975	50	temperate	Thomas, 1968	Froese and Pauly, 2022

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Elasmobranchi	*Lamna nasus*	Porbeagle	0.18	300	35	boreal	Aasen, 1963	Froese and Pauly, 2022
Elasmobranchi	*Squalus acanthias*	Spiny dogfish	0.09	160	75	temperate	Wood *et al.*, 1979	Froese and Pauly, 2022
Gadiformes	*Merluccius productus*	North Pacific hake	0.56	40		temperate	Pauly, 1980	Froese and Pauly, 2022
Gadiformes	*Albatrossia pectoralis*	giant grenadier	0.105	56.608	58	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Coelorinchus biclinozonalis*	two saddle rattail	0.67	54.83	15		Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Coelorinchus bollonsi*	Bollons's rattail	0.35	49.76	24		Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Coryphaenoides rupestris*	roundnose grenadier	0.11	32.4	60		Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Hymenocephalus italicus*	glasshead grenadier	0.645	5.3	9	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Lepidorhynchus denticulatus*	javelinfish	0.29	55.22	10		Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Macrourus berglax*	roughhead grenadier	0.25	56.69	20	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Macrourus carinatus*	ridge-scaled rattail	0.15	76.46	42	polar	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Merluccius australis*	southern hake	0.21	113.4	27	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Nezumia aequalis*	common Atlantic grenadier	0.94	9.6	9	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Trisopterus minutus*	poor cod	1.17	23	5	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Gadiformes	*Gadus morhua*	Atlantic cod	0.17	115.3	23	polar	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Gadiformes	*Gadus morhua*	Atlantic cod	0.18	200		boreal	Pinhorn, 1975	Froese and Pauly, 2022
Gadiformes	*Gadus morhua*	Atlantic cod	0.2	200		temperate	Swain *et al.*, 2009	Froese and Pauly, 2022
Gadiformes	*Gadus morhua*	Atlantic cod	0.4	200		temperate	Swain *et al.*, 2009	Froese and Pauly, 2022
Gadiformes	*Merluccius angustimanus*	Panama hake	0.84	40		tropical	Mathews, 1975	Froese and Pauly, 2022
Gasterosteiformes	*Gasterosteus aculeatus*	three-spined stickleback	1.06	5.08	4	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Gasterosteiformes	*Hippocampus guttulatus*	long-snouted seahorse	1.22	19.76	5.5	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Myctophiformes	*Benthosema glaciale*	glacier lantern fish	0.91	7.5	5	polar	Then *et al.*, 2015	Then *et al.*, 2015
Myctophiformes	*Gymnoscopelus nicholsi*	Nichol's lanternfish	0.61	15.1	7	polar	Then *et al.*, 2015	Then *et al.*, 2015
Myctophiformes	*Lampanyctodes hectoris*	lanternfish	1.58	7.01	3	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Myctophiformes	*Notoscopelus elongates*	lanternfish	0.8	11.91	6	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Myliobatiformes	*Urolophus paucimaculatus*	white spotted stingaree	0.445	50.05	10	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Rastrelliger kanagurta*	Indian mackerel	0.65	42	4	subtropical	Banerji, 1973	Froese and Pauly, 2022
Perciformes	*Scomber japonicus*	Chub mackerel	0.9	64	18	subtropical	Sekharan, 1975	Froese and Pauly, 2022
Perciformes	*Acanthurus bahianus*	ocean surgeonfish	0.083	18.22	31	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Acanthurus nigrofuscus*	brown surgeonfish	0.174	15.2	25	tropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Achoerodus gouldii*	western blue groper	0.086	77.7	70	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Amblygobius bynoensis*	Bynoe goby	4.05	11.71	1.03	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Amblygobius phalaena*	whitebarred goby	3.82	11.44	1.13	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Ammodytes dubius*	sand lance	0.885	26.2	10	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Ammodytes marinus*	Shetland sandeel	1.28	18.5	8	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Ammodytes tobianus*	small sandeel	1.1	16	7	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Argyrozona argyrozona*	Carpenter seabream	0.27	62.3	27	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Arripis trutta*	Australian salmon	0.8	58.4	7	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Bodianus frenchii*	foxfish	0.067	39.6	78	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Callionymus lyra*	dragonet	1.146	17.4	6	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Caulolatilus microps*	blueline tilefish	0.22	64.3	43	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Cephalopholis fulva*	coney	0.55	34		tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Cepola macrophthalma*	red bandfish	0.88	66.96	8	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Chaenodraco wilsoni*	spiny icefish	2.26	32.55	5	polar	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Champsocephalus gunnari*	mackerel icefish	0.56	68.8	8	polar	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Cheilinus undulatus*	humphead wrasse	0.11		30	tropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Chlorurus sordidus*	daisy parrotfish	0.49	15.821	9	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Choerodon venustus*	venus tusk fish	0.45	82.9	20	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Chromis chromis*	damselfish	1.07	14.2	9	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Chrysoblephus cristiceps*		0.2094	65.47	23	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Chrysoblephus laticeps*		0.2395	42.5	17	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Coris auricularis*	western king wrasse	0.54	37.8	10.5	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Coris julis*	rainbow wrasse	1.58	27.15	8	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Cromileptes altivelis*	humpback grouper	0.26	57.5	19	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Diplodus annularis*	annular seabream	0.49	20.37	7	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Diplodus capensis*	blacktail seabream	0.11	41.95	31	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Diplodus sargus*	sargo	1.33	41.7	10	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Diplodus vulgaris*	two banded bream	0.625	27.73	14	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Dissostichus eleginoides*	Patagonian toothfish	0.09	98.2	36	polar	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Epigonus telescopus*	black cardinalfish	0.034	70.8	104	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Epinephelus coioides*	estuary rockcod	0.29	108.2	22	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Epinephelus guttatus*	red hind	0.2	51.45	18	tropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Epinephelus malabaricus*	Malabar grouper	0.17	127.8	31	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Girella tricuspidata*	luderick	0.38	34.84	24	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Glaucosoma buergeri*	pearl perch	0.14	51.27	26	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Gobius vittatus*	striped goby	0.965	5.0545	4	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Gymnocranius audleyi*	collared large-eye bream	0.583	28.245	13	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Istigobius decorates*	decorated goby	7.92		0.73	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Istigobius goldmanni*	Goldman's goby	5.07	6.48	0.88	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Katsuwonus pelamis*	skipjack tuna	1.6	65.1	10	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lethrinus miniatus*	red throat emperor	0.368	52.06	25	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lethrinus nebulosus*	spangled emperor	0.146	57.31	30.75	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lichia amia*	leerfish	0.41	113.7	11	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lipophrys pholis*	shanny	0.79	17	6	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lithognathus aureti*	westcoast steenbras	0.35	70	28	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lopholatilus chamaeleonticeps*	golden tilefish	0.259	90.7	33	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus adetii*	hussar	0.24	26.52	24	tropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Lutjanus analis*	mutton snapper	0.13	87.44	40	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus argentimaculatus*	mangrove jack	0.13	65.95	52	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus carponotatus*	stripey, stripey bass, Spanish flag snapper	0.1994	31.3	20	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus erythropterus*	crimson snapper	0.15	58.45	32	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus griseus*	Gray snapper	0.35	71.7	24	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus jocu*	dog snapper	0.134	77.22	25	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus malabaricus*	scarlet seaperch	0.115	62.28	31	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus peru*	Pacific red snapper	0.345	97.32	31	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus quinquelineatus*	five-line snapper	0.15	20.69	31	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Lutjanus vitta*	Brown stripe snapper, brown stripe red snapper	0.3424	24.53	12	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Mycteroperca bonaci*	black grouper	0.16	130.62	33	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Nemipterus japonicas*	Japanese threadfin bream	0.52	30.54	4	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Nemipterus thosaporni*	palefin threadfin bream	1.73	24.5	5	tropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Notolabrus celidotus*	paketi, spotty	0.55	25.763	8	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Notolabrus parilus*	brownspotted wrasse	0.59	33.5	10.4	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Notothenia neglecta*	yellowbelly rockcod	0.36	39.6	18	polar	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Ocyurus chrysurus*	yellowtail snapper	0.56	45.09	14	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Pagrus pagrus*	red porgy	0.44	76.3	15	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Paralabrax clathratus*	kelp bass	0.287	69.8	33	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Patagonotothen brevicauda*	Patagonian rockcod	0.9175	23.31	7	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Pentapodus vitta*	butterfish	0.91	15.66	8	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Plagiogeneion rubiginosum*	rubyfish	0.035	47.7	100	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Plectropomus areolatus*	passionfruit trout	0.3995	76.4	14	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Plectropomus leopardus*	coral trout	0.147	71.19	18	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Plectropomus maculatus*	inshore coral trout	0.39	60	12	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Polydactylus macrochir*	king threadfin	0.119	122.2	21.9	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Polyprion oxygeneios*	hapuku	0.12	89	52	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Pomacanthus maculosus*	yellowbar angelfish	0.15	28.8	36	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Protonibea diacanthus*	blackspotted croaker, ghol	0.855	122.14	8	subtropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Pterogymnus laniarius*	panga	0.36	37.94	16	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Rhabdosargus sarba*	tarwhine	0.3342	30.284	14	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Rhomboplites aurorubens*	vermillion snapper	0.37	65	14	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Scarus frenatus*	bridled parrotfish	0.24	25.543	20	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Sciaenops ocellatus*	red drum	0.04	111.4	56	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Scomberomorus cavalla*	king mackerel	0.46	106.7	14	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Scomberomorus commerson*	narrow-barred Spanish mackerel	0.62	141.25	14	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Semicossyphus pulcher*	California sheephead	0.2	56.96	29	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Seriola dumerili*	greater amberjack	0.61	164.8	17	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Serranus cabrilla*	comber	0.68		7	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Sparisoma viride*	stoplight parrotfish	0.274	28.06	9	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Spicara maena*	blotched picarel	1.18	24.82	8	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Spicara smaris*	picarel	0.98	22.76	6	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Stegastes arcifrons*	island major	0.1471	10.38	27	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Stegastes beebei*	whitetail major	0.2994	9.36	19	tropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Stegastes rectifraenum*	Cortez damselfish	0.402	10.73	11	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Symphodus roissali*	five-spotted wrasse	1.71	16.53	3	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Symphodus tinca*	peacock wrasse	0.25	42.24	13	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Thunnus albacares*	yellowfin tuna	1.085	166.4	7	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Thunnus maccoyii*	southern bluefin tuna	0.22	183.2	41	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Thunnus obesus*	bigeye tuna	0.48	169	16	tropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Trachurus declivis*	jack mackerel	0.56	46.4	16	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Trachurus japonicas*	Japanese jack mackerel	0.99	38.6	5	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Trachurus novaezelandiae*	jack mackerel	0.18	37.7	28	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Valenciennea muralis*	mural goby	4.87	10.61	0.99	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Perciformes	*Atractoscion nobilis*	White seabass	0.21	166		temperate	Thomas, 1968	Froese and Pauly, 2022
Perciformes	*Nemadactylus macropterus*	Tarakihi	0.03	70		temperate	Vooren, 1977	Froese and Pauly, 2022
Perciformes	*Nemipterus marginatus*	Red filament threadfin bream	1.14	20		tropical	Pauly and Martosubroto, 1980	Froese and Pauly, 2022
Perciformes	*Nemipterus marginatus*	Red filament threadfin bream	1.73	20		tropical	Pauly and Martosubroto, 1980	Froese and Pauly, 2022

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Perciformes	*Neothunnus macropterus*	yellowfin tuna	0.77	210		tropical	Hennemuth, 1961	'Australian Fisheries Management Authority', n.d.
Perciformes	*Pomatoschistus minutus*	Sand goby	0.01	4		temperate	Fonds, 1973	Froese and Pauly, 2022
Perciformes	*Pseudosciaena diacanthus*	Blackspotted croaker	0.83	150		subtropical	Rao, 1968	Froese and Pauly, 2022
Perciformes	*Rastrelliger kanagurta*	Indian mackerel	0.37	42		tropical	Sudjastani, 1962	Froese and Pauly, 2022
Pleuronectiformes	*Atheresthes stomias*	arrowtooth flounder	0.19	101.5	25	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Hippoglossoides platessoides*	American plaice	0.18	60	32	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Hippoglossus hippoglossus*	Atlantic halibut	0.22	169.65		boreal	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Hippoglossus stenolepis*	Pacific halibut	0.198	134.5	55	polar	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Limanda ferruginea*	yellowtail flounder	0.256	55.6	15	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Parophrys vetulus*	English sole	0.39	37.22	16	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Pseudopleuronectes americanus*	winter flounder	0.3	46.86	11	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Pleuronectiformes	*Eopsetta jordani*	Petrale sole	0.21	53		temperate	Ketchen and Forrester, 1966	Froese and Pauly, 2022
Pleuronectiformes	*Hippoglossoides platessoides*	American plaice	0.28	82		temperate	Bakken, 1987	Froese and Pauly, 2022
Salmoniformes	*Salvelinus alpinus*	Arctic char	0.16	107		polar	Moore, 1975	Froese and Pauly, 2022
Scorpaeniformes	*Eutrigla gurnardus*	grey gurnard	1.07	26.4	8	subtropical	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	Species	Common Name	M (y-1)	Max Length (cm)	Max Age (y)	Region	Source for M	Source for length and age
Scorpaeniformes	*Hemilepidotus jordani*	yellow Irish lord	0.18	46.3	28	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes aleutianus*	rougheye rockfish	0.037	54.74	205	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes alutus*	Pacific ocean perch	0.048	42.6	100	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes brevispinis*	silvergray rockfish	0.0483	56.8	80	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes ciliatus*	dark rockfish	0.073	43.5	61	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes crameri*	darkblotched rockfish	0.014	42.3	105	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes diploproa*	splitnose rockfish	0.04	31.98	84	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes elongatus*	greenstriped rockfish	0.15	33.8	46	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes emphaeus*	Puget Sound rockfish	0.44	15.406	13	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes flavidus*	yellowtail rockfish	0.07	48.6	53	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes goodei*	chilipepper	0.41	45.925	16	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes melanops*	black rockfish	0.2	50.68	42	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes paucispinis*	bocaccio	0.434	82.17	14	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes pinniger*	canary rockfish	0.038	53.3	84	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes proriger*	redstripe rockfish	0.1	38.3	42	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes reedi*	yellowmouth rockfish	0.1425	46.3	72	temperate	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.4 *continued*

Order	**Species**	**Common Name**	**M (y-1)**	**Max Length (cm)**	**Max Age (y)**	**Region**	**Source for M**	**Source for length and age**
Scorpaeniformes	*Sebastes ruberrimus*	yelloweye rockfish	0.0174	65.96	121	subtropical	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastes zacentrus*	sharpchin rockfish	0.07	34.9	46	temperate	Then *et al.*, 2015	Then *et al.*, 2015
Scorpaeniformes	*Sebastolobus alascanus*	shortspine thornyhead rockfish	0.07	70	89	boreal	Then *et al.*, 2015	Then *et al.*, 2015
Tetraodontiformes	*Balistes vetula*	queen triggerfish	2.6	45		tropical	Then *et al.*, 2015	Then *et al.*, 2015
Zeiformes	*Allocyttus niger*	black oreo	0.044	38.55	142	temperate	Then *et al.*, 2015	Then *et al.*, 2015

Appendix 2.5 References on natural mortality rates for egg, larval, juvenile, and adult marine fishes.

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Chapter 3 – Recruitment pulses of age-0 and age-1 Atlantic cod (*Gadus morhua*) in a coastal ecosystem demonstrate low winter growth and variable size-structured survival

3.1 Abstract

Juvenile Atlantic cod (*Gadus morhua*) in coastal Newfoundland settle to nearshore habitats in multiple (3-6) discrete events, or pulses, annually. These pulses produce a size-structured population in the first year of life that varies from year to year. Understanding the pulse structure for each year-class has important implications for cod survival and fisheries management. Recent studies on age-0 Atlantic cod assigned pulse structure through visual determinations, using histograms and scatter plots. However, this approach can be subjective and cannot track pulse structure through to age-1. We use finite mixture distribution models to classify pulse structure for age-0 and age-1 Atlantic cod using length data from the Newman Sound coastal juvenile survey (1996-2019), illustrating the approach with the 2018 cohort. Following assignment of pulses, we examine pulse structure across the entire 23-year time series to evaluate changes in winter growth and mortality across recruitment pulse and annual cohort. Our analysis shows that finite mixture distribution models accurately identify pulse structure of age-0 cod and age-1 cod. Furthermore, winter growth varies only among annual cohorts and not among pulses, whereas winter mortality varies by both recruitment pulse and annual cohort. Determining pulse structure enables better understanding of size-structured growth and survival of age-0 and age-1 Atlantic cod, with potential applicability to other species with size-structured recruitment pulses.

3.2 Introduction

Numerous studies have identified size-structure as an important driver of natural mortality of early life stages of fishes (Werner and Gilliam, 1984; Sogard, 1997; Huss *et al.*, 2008). Size plays a role in susceptibility to predation (Linehan *et al.*, 2001; Andersen *et al.*, 2009) and energetic capacity of fishes (Sogard and Olla, 2000; Mogensen and Post, 2012). Although size-frequency often closely reflects year class within populations (Macdonald and Pitcher, 1979), multiple settlement pulses in some fish populations result in broad size-frequency distribution within a single annual cohort. For example, plaice (*Pleuronectes platessa*; Geffen *et al.*, 2011), winter flounder (*Pseudopleuronectes americanus*; Dolan *et al.*, 2021), bluefish (*Pomatomus saltatrix*; Morley *et al.*, 2013), and Newfoundland coastal Atlantic cod (*Gadus morhua*; Methven and Bajdik, 1994; Ings *et al.*, 2008) populations all produce multiple distinct pulses in a single year. In some species, pulses are days apart (i.e., American shad, *Alosa sapidissima*; striped bass, *Morone saxatilis*) and can only be detected through otolith analysis or extensive sampling (Crecco and Savoy, 1985; Rutherford and Houde, 1995; Limburg, 1996). Multiple settlement pulses exemplify temporally split cohorts (Secor, 2007), known as pulses throughout this study, and may represent a bet-hedging life history strategy. Given that multiple settlement pulses can result in different survival and growth conditions (Sogard and Able, 1992; Dolan *et al.*, 2021), treating multiple pulses as a single population can limit understanding of growth and survival during a critical life stage.

Age-0 Atlantic cod in coastal Newfoundland settle in 2-6 recruitment pulses each year (Methven and Bajdik, 1994; Grant and Brown, 1998; Ings *et al.*, 2008). In contrast, plaice, winter flounder, and bluefish settle in only 2-3 recruitment pulses (Geffen *et al.*, 2011; Morley *et al.*, 2013; Dolan *et al.*, 2021). Despite the high number of recruitment pulses in cod, length-frequency distributions can clearly separate settlement pulses (Grant and Brown, 1998). Atlantic cod recruitment pulses coincide with onshore wind events (Ings *et al.*, 2008), and produce distinct size modes throughout their first season (Gregory *et al.*, 2019). Multiple recruitment pulses have not been identified in other Atlantic cod populations at the juvenile stage. However, whether recruitment pulses are specific to coastal Newfoundland cod, winter flounder (Dolan *et al.*, 2021), and European plaice (Geffen *et al.*, 2011) remains unclear, or if limited sampling has missed multiple recruitment pulses in other populations.

Improved understanding of fish ecology requires knowledge of size structure within a population context, and finite mixture distribution models provide a reliable technique for determining distinct groups within a multi-modal distribution (Macdonald and Pitcher, 1979). Fisheries science has a long history of using mixture models to classify age groups in fisheries science (Titterington *et al.*, 1985). Mixture models use compound statistical distributions in mixed populations for which each subcomponent has a different probability density function (Everitt, 1996). Advanced technology and statistical programming have increased the accessibility of Maximum Likelihood Estimation (MLE) for finite mixture models to estimate parameters of the distributions. Mixture models offer an important tool in assessing size-structure within a population because of their cluster-based approaches for instances with undefined subpopulations (McLachlan and Peel, 2000).

Mixture models offer an improvement over previous assessments based on graphical interpretation only. Inclusion of multiple pulses, especially across years, can provide improved assessment of population trajectories and their drivers. In this study, we therefore use finite mixture models to determine pulse structure of age-0 and age-1 Atlantic cod, highlighting the utility of that knowledge by estimating and evaluating winter growth and mortality rates by pulse across a 25-year time series.

3.3 Methods

3.3.1 Data

We use length and abundance data from standardized coastal juvenile beach seine surveys (1998-2020) conducted by Fisheries and Oceans Canada at 12 sites in Newman Sound, Newfoundland (Fig. 3.1). Pooling abundances from the 12 sites yielded a sufficient sample size for model reliability. Length data (mm SL) provided the primary source for fitting finite mixture distribution models, whereas abundance data (catch · haul^{-1}) enabled us to determine pulse strength.

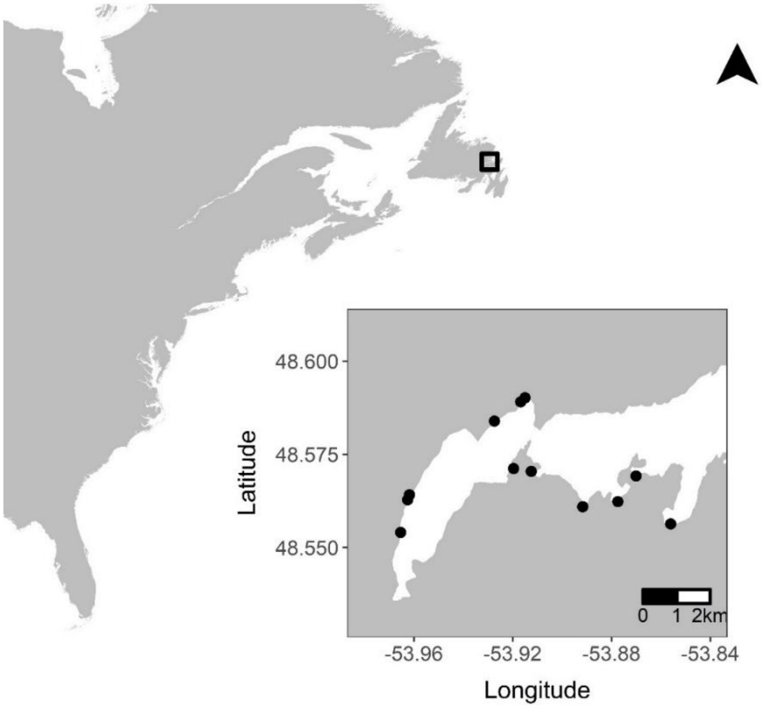

Figure 3.1. Map of 12 sites in Newman Sound, Newfoundland, Canada. Juvenile Atlantic cod (*Gadus morhua*) were sampled by a boat-deployed beach seine from 1998-2019 during May and July to November.

3.3.2 Finite mixture distribution models

Mixture models were derived using the *mixdist* package in R (Macdonald and Du, 2018; R Core Team, 2021), which fits finite mixture distributions using MLE and a combination of Newton-type and expected-maximization (EM) algorithms. Newton-type algorithms find roots and solve partial differential equations (Du, 2002). EM algorithms find MLE parameter estimates of a distribution for incomplete data sets with missing values (Blimes, 1998). We use constraints on parameters because of small sample sizes to avoid over parameterization (Estes *et al.*, 2015).

Estimation of one parameter enables removal or adjustment of constraints when estimating the remaining parameters.

The use of iterative algorithms requires estimating the initial parameters to provide a starting point for the algorithm (Du, 2002); multiple minimization iterations can then develop the final parameter estimates. Each component requires estimation of three parameters: the mean, μ, the standard deviation, σ, and the proportion, π. It is not always possible to estimate all the parameters, especially with small sample size or overlapping components (Du, 2002; Estes *et al.*, 2015). For this reason, we reduced the number of estimated parameters by assuming constraints on π and σ (Macdonald and Pitcher, 1979). First, that π adds to 1 to place a natural constraint on proportions. The second constraint focuses on standard deviations, σ; we assume a constant coefficient of variation (CCV). We derive all initial μ parameter estimates from size frequency distributions and probability density functions and assume a gamma distribution for all mixtures.

3.3.3 Pulse assignment

We assigned mixture distributions (μ, σ, and π) to age-0 and age-1 cod for each sampling interval across the entire time series. To illustrate the approach, we review the 2018 cohort assignment, which provided a model year with sufficient abundance and a clearly defined pulse structure. We used the mixture distribution groups as a baseline for pulse assignment and determined final pulse assignment based on growth trajectories and abundance, evaluated through visual assessments and abundance data.

3.3.4 Statistical analysis

We calculated specific growth rates (SGR) for Pulse 2 and Pulse 3 from 1998 to 2019, noting that Pulse 1 calculations were impossible because of the complete absence of Pulse 1 during

May sampling of age-1 juveniles in many years. We calculated specific growth rate for length (SGR_L; Hawkins *et al.*, 1985) as:

$$SGR_L = (\ln SL_2 - \ln SL_1) \cdot (t_2 - t_1)^{-1} \cdot 100, \qquad (1)$$

with SL_2 and SL_1 as mean standard length at times t_2 and t_1 with time t_1 as day 0, selected as the final day of sampling in autumn, and t_2 as the number of days between day 0 (t_1) and the spring sampling (May). We then calculated percent daily instantaneous mortality ($\%M \cdot d^{-1}$) as:

$$\%M \cdot d^{-1} = \ln(N_{i+t}/N_i) \cdot t^{-1} \cdot 100. \qquad (2)$$

with catch per haul (N) at time i in October and time $i+t$ in July. Sampling dates spanned approximately 275 (t) days. We selected July as our post-winter sampling date because it typically represents a reliable estimate of abundance each year. Variable temperatures in May (-0.4 – 9.8 °C) resulted in highly inconsistent abundances.

We evaluated the effect of pulse structure and cohort on growth (SGR) and percent daily instantaneous mortality ($\%M \cdot d^{-1}$) using two general linear models with Gaussian error distributions, treating pulse and cohort as categorical explanatory variables. SGR or $\%M \cdot d^{-1}$ were the response variables for their respective models. All analyses used R statistical programming language (R Core Team, 2021).

3.4 Results

3.4.1 2018 Age-0 pulse structure

The 2018 cohort began with a single mode distribution in August and September, and a second mode developed in October. Figure 3.2 provides an example of modal distribution for age-0 cod. The multi-modal distribution remained consistent across bi-weekly seining trips, and initially predicted a total of three groups by December (Fig. 3.3). Because we analyzed the intervals in isolation, the models could not capture growth rate over time. Once we determined initial assignments, we adjusted them based on known biological constraints (i.e., a fish cannot typically shrink in length). September 24-25 illustrates an introduced pulse that the model did not recognize. The probability density function detected a start of a mode (Fig. 3.2). Additionally, a decrease in length occurred from September 24-25 to October 9-10, indicating the onset of settlement of a new pulse (Fig. 3.3). Pulses are generally numerically weaker after initial settlement (most often due to predation mortality), resulting in the model overlooking emergent pulses due to small sample sizes (Table 3.1). The models guide assignments, allowing us to assign pulses within biological constraints while limiting potential biases. Potential biases include combining multiple pulses together, resulting in too few pulses, or dividing pulses beyond the modal distribution, resulting in too many pulses. Based on initial mixture distribution assignments and growth constraints, we identified four pulses for the 2018 cohort (Fig. 3.4).

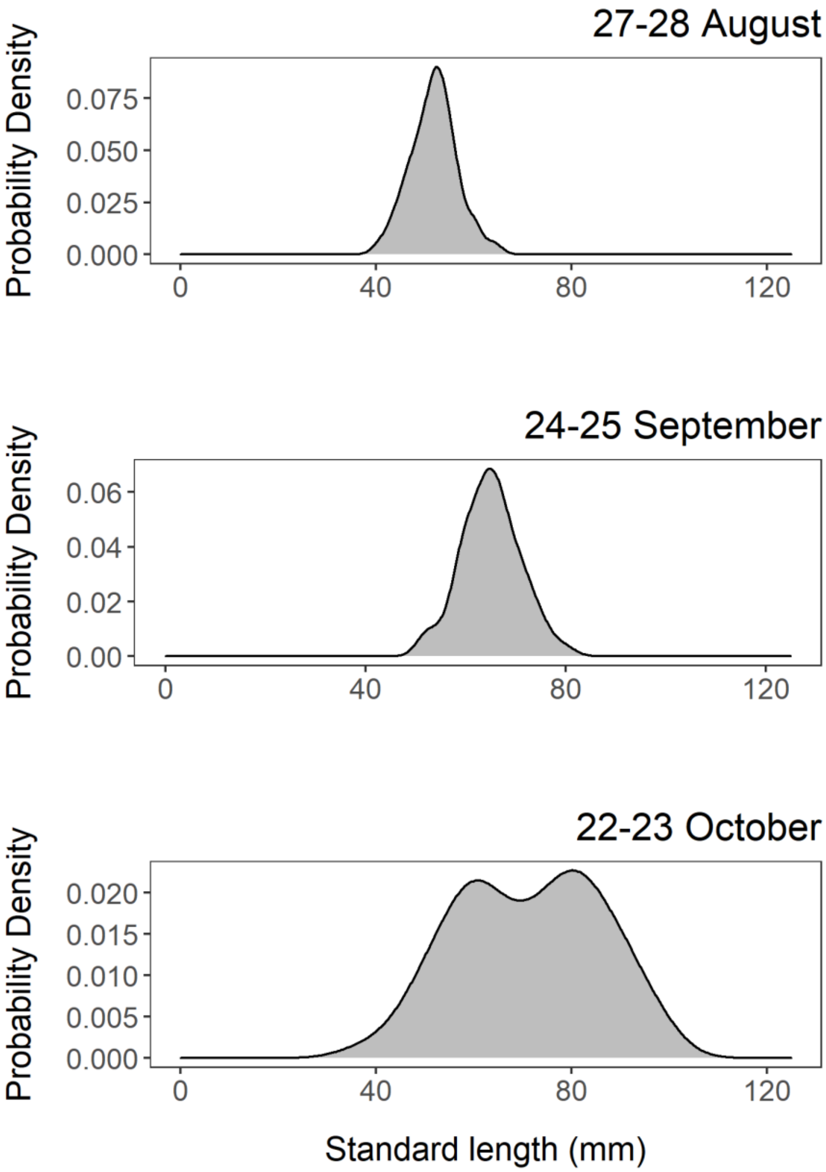

Figure 3.2. Probability density functions of age-0 Atlantic cod (*Gadus morhua*) standard length (mm) sampled across three months (August, September, October 2018) in Newman Sound, Newfoundland.

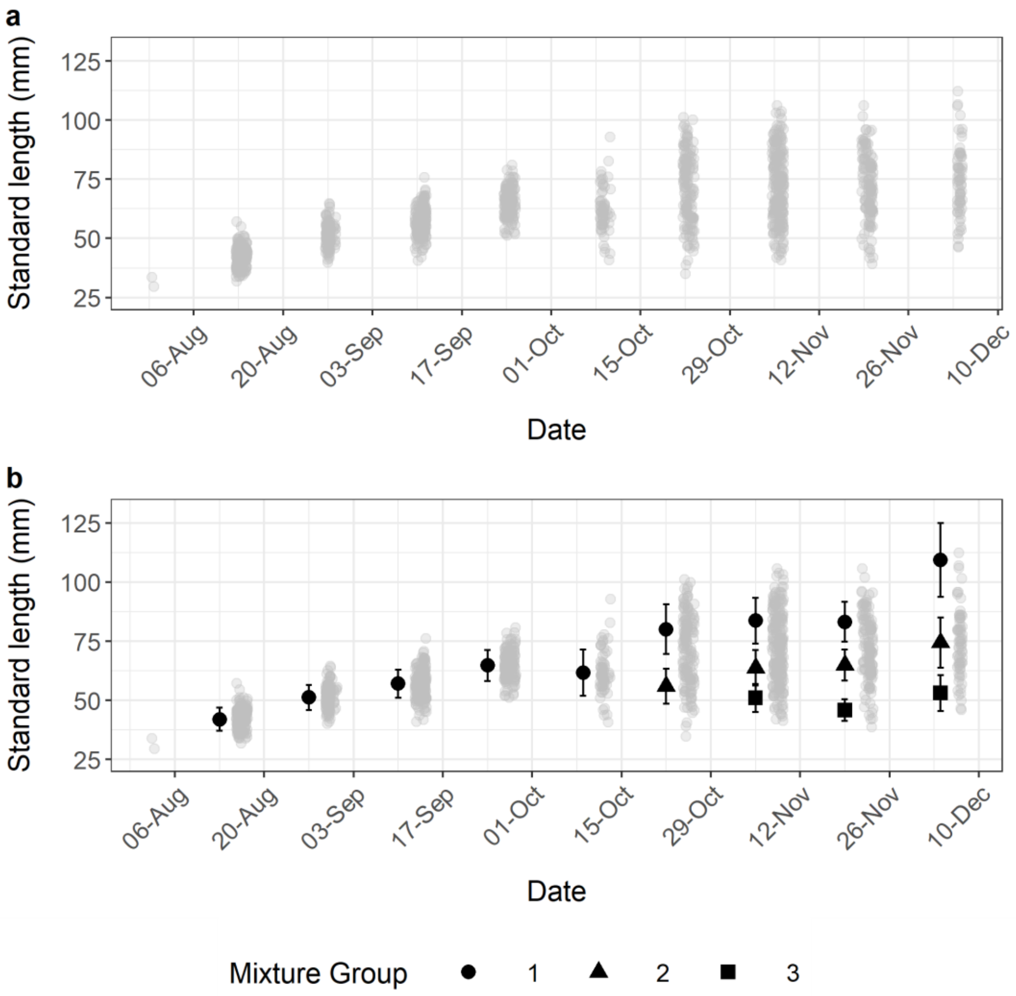

Figure 3.3. Standard length (mm) of age-0 Atlantic cod (*Gadus morhua*) from July 2018 to December 2018, in Newman Sound, Newfoundland, with (a) no assignments and (b) mixture groups derived from mixture distribution models.

Table 3.1. Catch · haul^{-1} of age-0 and age-1 Atlantic cod (*Gadus morhua*) for each pulse the 2018 cohort from July 2018 to May 2019 in Newman Sound, Newfoundland.

Date	**Age**	**Pulse 1**	**Pulse 2**	**Pulse 3**	**Pulse 4**	**Pulse 5**
2018-07-30	0	0.17				
2018-08-13	0	12.75				
2018-08-27	0	10.25				
2018-09-10	0	15				
2018-09-24	0	11.25	0.58			
2018-10-09	0	1.11	3.42	0.48		
2018-10-22	0	5.55	4.08	1.96	0.24	
2018-11-05	0	6.55	7.38	3.07	0.41	
2018-11-19	0	2.73	3.03	3.33	0.83	
2018-12-04	0	0.73	1.911	2.55	1.18	
2019-05-07	1	0.00	4.67	6.209	0.00	19.04

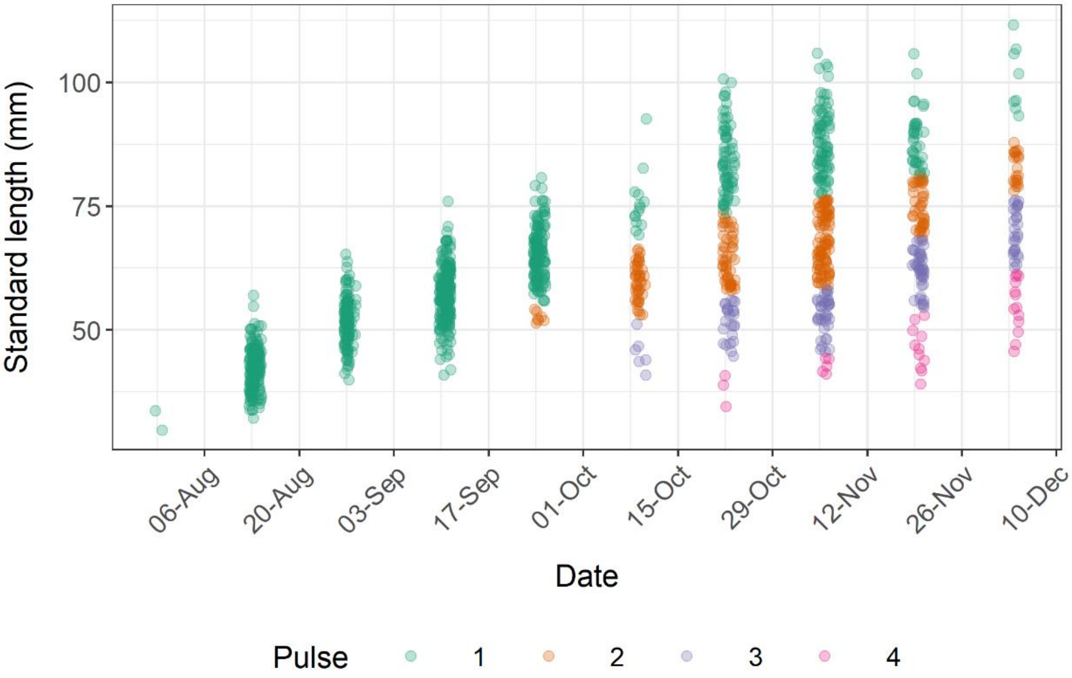

Figure 3.4. Final pulse assignment for age-0 2018 Atlantic cod (*Gadus morhua*) cohort from July to December 2018 in Newman Sound, Newfoundland.

3.4.2 2018 Age-1 pulse structure

Growth and abundance determined age-1 pulse assignments, and growth constrained pulse assignments and the assumption of ≥0 growth rates. Based on growth trajectories, Pulse 4 would have had to shrink to line up with mixture group 3 (Fig. 3.5). We thereby inferred the presence of a fifth pulse. Based on the mixture model results, we identified 3 mixture groups present in the spring. The new fifth pulse described above comprised one of those groups, leaving two more groups to assign. Given growth constraints, we determined that Pulse 1 was absent by the spring, leaving Pulses 2, 3, and 4. Pulse 4 was numerically weak entering winter, relative to Pulse 2 and Pulse 3 (Table 3.1), and likely died out or "merged" with Pulse 3, leaving the two indistinguishable.

In cases where pulses merged, we maintained the numerically stronger pulse. In this case, Pulse 3 persisted through winter (Fig. 3.6).

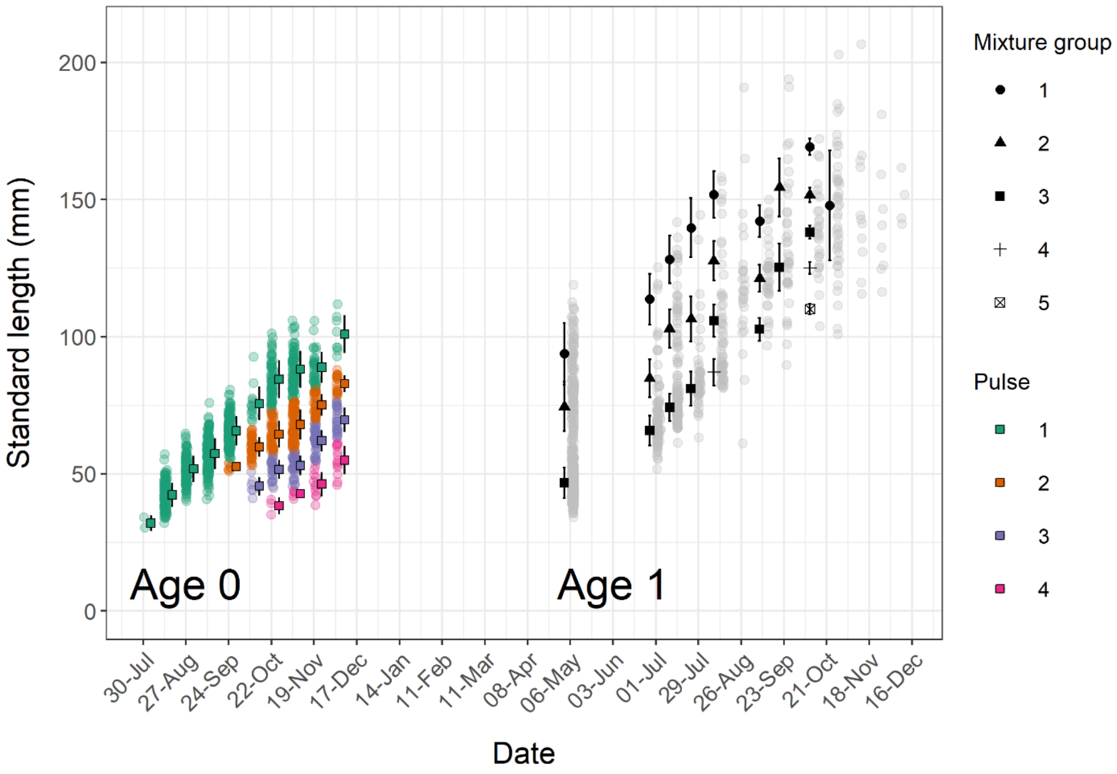

Figure 3.5. 2018 Atlantic cod (*Gadus morhua*) cohort from age-0 (colours) and age-1 (grey and black) from Newman Sound, Newfoundland. The coloured boxes represent the mean standard length for each pulse. Error bars show standard deviations. The black solid shapes represent the mixture group derived from finite mixture distribution models for age-1 cod. Error bars represent standard deviation.

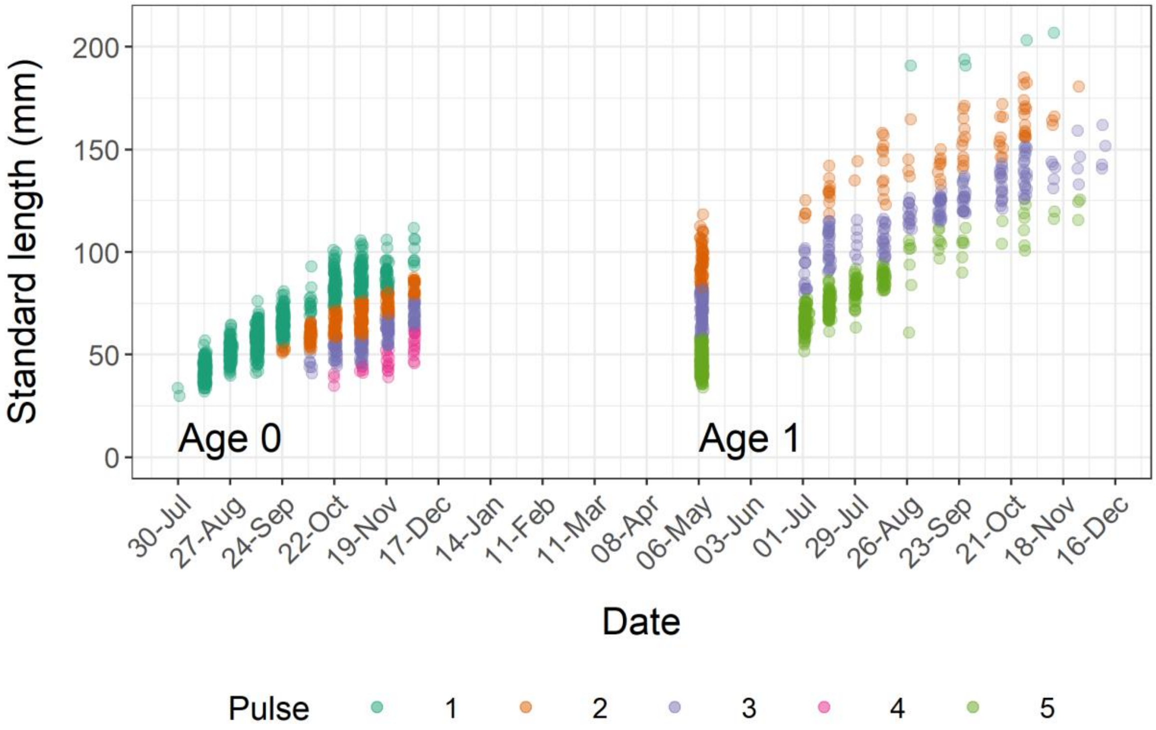

Figure 3.6. Final pulse assignments for the 2018 Atlantic cod (*Gadus morhua*) cohort from age-0 (colours) and age-1 from Newman Sound, Newfoundland. The coloured points represent the pulse assignment for age-0 and age-1 cod.

3.4.3 Winter growth and mortality

Applying this pulse assignment approach across the broader data set, we estimated standard growth rate (SGR) for Pulse 2 and Pulse 3 across the winter period for the entire Newman Sound time series (1998-2019; Fig. 3.7). These growth rates were almost zero. General linear models showed that SGR varied by cohort (F-value = $5.95_{16,9}$, p = 0.005) but not by pulse (F-value = $0.779_{1,9}$, p = 0.4). The mean SGR of 0.093 % · d^{-1} (± 0.012) in Pulse 2 was slightly greater than the mean SGR of 0.077 % · d^{-1} (± 0.012) in Pulse 3. We observed the highest SGR for the 2002 cohort (0.203 ± 0.023 % · d^{-1}), followed by the 2006 cohort (0.175 ± 0.041 % · d^{-1}). The lowest SGR occurred in the 1998 (-0.062 ± 0.041 % · d^{-1}) and the 2015 (-0.034 ± 0.028 % · d^{-1}) cohorts.

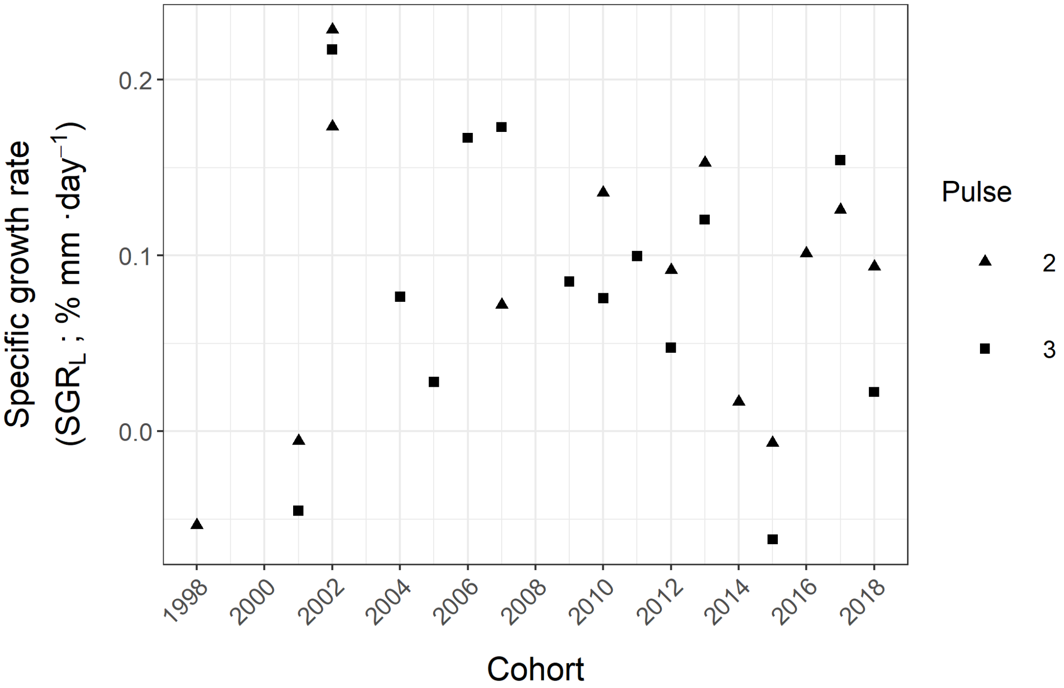

Figure 3.7. Estimates of Atlantic cod (*Gadus morhua*) winter specific growth rate (SGR) during their first winter for Pulse 2 (triangle) and Pulse 3 (square) groups for each annual cohort (1998-2018) in Newman Sound, Newfoundland.

Mortality varied by cohort ($F = 5.04_{14,7}$, LR = 3.46 · 10^{12}, p = 0.019) and by pulse ($F = 0.49_{2,7}$, LR = 3.68 · 10^4, p=0.047). The mean mortality rate of 0.019% · d^{-1} (± 0.138) in Pulse 3, was considerably smaller than the mean mortality rate of 0.425% · d^{-1} (± 0.167) in Pulse 1 and the mean mortality rate of 0.623% · d^{-1} (± 0.148) in Pulse 2. We also observed strong variation among cohorts, with the lowest mortality in the 2008 cohort (-1.078 ± 0.369% · d^{-1}), and highest mortality in the 2002 (1.306 ± 0.369 % · d^{-1}), 2011 (1.461 ± 0.356% · d^{-1}), and 2014 (1.511 ± 0.360% · d^{-1}) cohorts (Fig. 3.8).

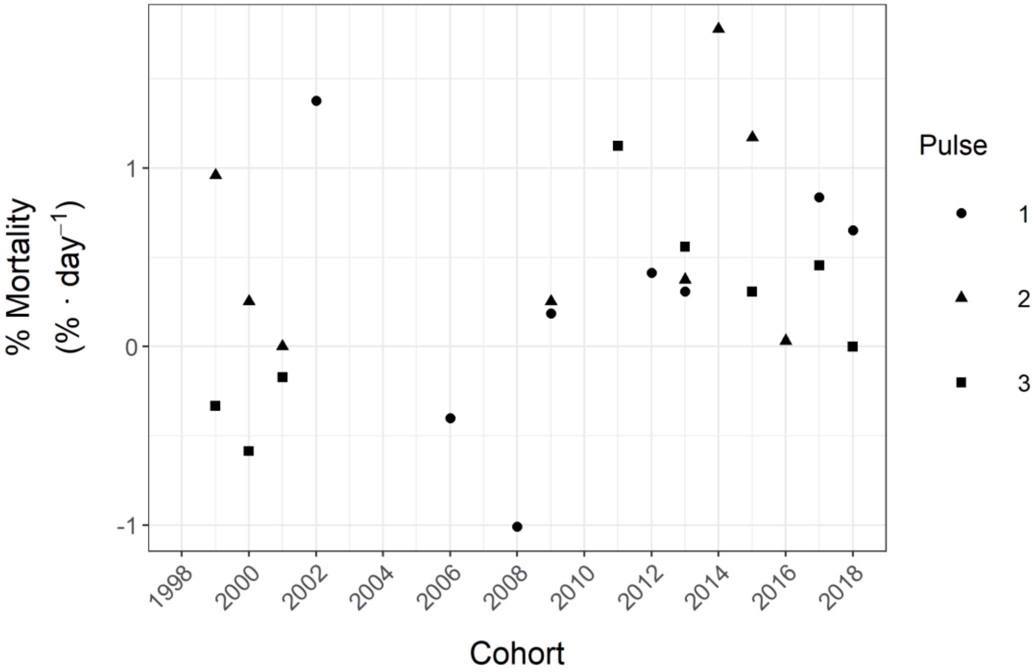

Figure 3.8. Estimates of Atlantic cod (*Gadus morhua*) winter natural mortality rate during their first winter for Pulse 1 (circle) Pulse 2 (triangle) and Pulse 3 (square) groups for each annual cohort (1998-2018) in Newman Sound, Newfoundland.

3.5 Discussion

Our analysis highlights a methodology to identify pulse structure in a species with multiple recruitment pulses each year. Finite mixture distribution models help remove the guesswork and eliminate observer bias in size classification for species with multiple settlement pulses. Importantly, the mixture models should not be applied indiscriminately; they do not provide a definitive result, and do not eliminate the need to understand growth and recruitment structure to balance mathematical and biological inferences. Previous recruitment studies classified Atlantic cod pulses for age-0, but not age-1 (e.g., Gregory *et al.*, 2004, 2018), but applying mixture models to determine pulse structure post-winter enables analysis of winter population dynamics (e.g., growth, survival). In this study, we calculated and compared growth and mortality rates of pulses from age-0 through to age-1. We were able to estimate winter specific growth rate (SGR) and daily mortality ($\% \cdot d^{-1}$), providing evidence of bet-hedging population dynamics in the first year of life in a marine fish.

Previous studies documented multiple recruitment pulses in age-0 cod (Methven and Bajdik, 1994; Grant and Brown, 1998; Ings *et al.*, 2008), but application of mixture models provides guidance in pulse assignments and limits potential bias. Previous studies identified multiple recruitment pulses through visual inspection of length-frequency histograms and scatter plots (Gregory *et al.*, 2004), or through otolith and catch data (Grant and Brown, 1998; Ings *et al.*, 2008; Geffen *et al.*, 2011); however, more recent research used parametric distributions to determine settlement pulses (Dolan *et al.*, 2021). Mixture distribution models take away some of the "guesswork" when 3 or more underlying pulses occur and provide a framework to build from. Understanding age-0 pulse structure can provide important insights into ecological dynamics such as growth, survival, and condition that may vary based on size or settlement time (Geissinger *et al.*, 2021, 2022).

Identifying age-1 pulses was not possible for this population until now, noting limited evidence of identifying pulse structure though age-1 in other populations. Previous studies that examined winter population dynamics in multi-pulsed populations, such as plaice, did not evaluate growth or mortality based on pulse group (Nash *et al.*, 1992; Nash and Geffen, 2000). Understanding population dynamics on a scale of recruitment pulses compared to annual cohorts can enable better understanding of the influence of size and seasonality on marine populations. Multiple pulses provide an increased opportunity for a population to thrive in conditions of high annual and within-season variability (Dolan *et al.*, 2021), but the circumstances that promote optimal growth and survival remain largely unknown.

Characterizing pulse structure from age-0 to age-1 has direct application to ecological studies, noting the important, but poorly understood role of overwinter survival in marine fishes. Size-structure plays an important role in winter growth and survival in freshwater (Pangle *et al.*, 2004; Morley *et al.*, 2013) but fewer studies have considered marine ecosystems (Cowan, 2002; Hurst, 2007; Sewall *et al.*, 2019). To understand better the role size plays in growth and survival overwinter requires appropriate classification of pulses before and after the winter period. Finite mixture distribution models allowed us to characterize age-1 pulse structure, thereby opening a door to evaluate the role that size plays in age-0 to age-1 populations over winter. This approach is especially important for species with multiple recruitment pulses annually, noting very limited understanding of the benefit of multiple pulses (i.e., early vs. late settlement).

Limited growth occurred overwinter, with little year-to-year variation. SGR varied annually but not between Pulse 2 and Pulse 3. The relatively low SGR aligns well with regional growth potential models for Newfoundland cod, which estimated near zero growth potential (Laurel *et al.*, 2017). Despite SGR close to 0 ($-0.6 – 0.23\% \cdot d^{-1}$), the annual variation we observed indicates potential biotic and abiotic influences on winter growth. The amount of food available in the system overwinter likely impacts annual growth (Geissinger *et al.*, 2021). Prior to winter, environmental conditions can result in differential growth and mortality patterns among populations with multiple recruitment pulses, such as when and where larvae settle to the seabed from the pelagia (Sogard and Able, 1992; Dolan *et al.*, 2021). However, in the case of cod, it appears that once they reach winter, similar environmental constraints may result in similar low growth rates across pulses.

Winter mortality varied with recruitment pulse and annual cohort. These results coincide with pulse-based mortality observed in autumn for plaice and winter flounder (Geffen *et al.*, 2011;

Dolan *et al.*, 2021). Our results highlight the presence of size-structured mortality in marine systems overwinter. However, we did not observe a clear pattern regarding mortality among pulses, noting strong annual variation with low mortality in Pulse 1 fish in some years, and low mortality in Pulse 3 fish in other years. Years with imprecise mortality estimates merit some consideration. For example, in 2008, a pulse 1 mortality rate close to -1 indicated 100% increase in fish overwinter. This estimate could occur from low abundance, which increases error and uncertainty around estimates. Emigration could also skew estimates. Pulse 1 juveniles tend to be larger and may move out of eelgrass habitat earlier in the season. Estimates in Pulse 3 fish below $0\ \% \cdot d^{-1}$ could reflect immigration past our sampling dates. These challenges highlight the importance of evaluating populations at a finer scale.

Variable survival among pulses suggests a bet-hedging strategy. Multiple recruitment pulses represent a bet-hedging strategy because not all juveniles experience the same biotic and abiotic stressors. This variation could give different pulses an advantage from year to year. Bet-hedging requires extensive energy from spawning (Smith *et al.*, 1990; Lambert and Dutil, 2000) but bet-hedging strategies, such as multiple recruitment pulses, can benefit a population by spreading out resources and ensuring at least one recruitment pulse survives to the following year. In this case study, we showed higher survival in pulse 1 fish in some years, but higher survival in pulse 2 or pulse 3 fish in other years. Multiple pulses spread out over time reflects a portfolio effect (Schindler *et al.*, 2015). Bet-hedging life history patterns allow a species to increase their survival and recruitment by spreading out their resources (offspring) through trade-offs such as reduced abundance over space or time (Starrfelt and Kokko, 2012). Bet-hedging life-history patterns are common across marine species, such as the multiple spawning events that result in multiple pulses of larval fish (Secor, 2007). However, few studies address bet-hedging impacts on juvenile life stages (but see, Dolan *et al.*, 2021). As protracted spawners, Atlantic cod utilize a risk-spreading strategy over time (Fogarty *et al.*, 2001; Secor, 2007). At the juvenile stage, recruitment pulses become distinct when pelagic juveniles settle to demersal habitats during downwelling events (Ings *et al.*, 2008). Strong annual variation in mortality between pulses indicates a need to consider additional biotic and abiotic factors to understand the effect of pulse structure on winter survival. Size, energetics, and temperature all influence mortality in aquatic systems (Farley *et al.*, 2016) and may explain both annual and size-structured variation in age-0 and age-1 Atlantic cod.

Our study highlights the benefits of characterizing pulse structure in understanding population dynamics. Pulse estimates enable year-to-year assessment of growth and mortality rates at a finer population scale. Although individual-based growth methods, such as otolith analysis, enable more fine-scaled estimates of growth, our approach improves population metrics (i.e., growth and mortality estimates) while enabling investigation of population components separately. Our case study did not account for spatial variation in recruitment pulses and assumes that settlement pulses are associated with onshore wind events (Ings *et al.*, 2008), which would result in consistent settlement time throughout a region. However, future research should determine whether spatial differences exist in recruitment pulses throughout a bay or region. Bet-hedging can be captured by temporal and/or spatial distance between recruitment pulses (Starrfelt and Kokko, 2012, Dolan *et al.*, 2021), with potentially important implications for survival and population assessments within a year-class.

It is important to identify and understand multiple recruitment pulses and their potential impacts on growth and survival. Estimating natural mortality can be challenging, especially during winter when sampling gaps often occur. However, assessing mortality based on settlement pulses can help determine the ecological benefits of bet hedging. Under the bet-hedging approach, an early pulse does not always confer optimal survival (Geissinger *et al.*, 2022, *in review*), pointing to the importance of considering multiple pulses in population and recruitment studies.

3.6 Acknowledgements

This research was sponsored by the Natural Sciences and Engineering Research Council of Canada through the NSERC (Canadian Healthy Oceans Network CHONe-I & II and two Strategic Projects grants), and its Partners: Department of Fisheries and Oceans Canada (including Productive Capacity, Environmental Science Strategic Research Fund, Atlantic Cod Science, Strategic Program for Ecosystem Research and Advice, Centre of Expertise for Aquatic Habitat Research; and Marine Conservation Targets programs) and INREST (representing the Port of Sept-Îles and City of Sept-Îles, Quebec), Environment Canada (Environmental Innovations Program - Green Plan), Parks Canada (Protected Areas Program; Species-at-Risk Fund), and Memorial University of Newfoundland. We thank over 250 MUN graduate and senior undergraduate students, DFO technical and biological support personnel, Parks Canada staff and other volunteers who contributed to this 25-year time series, and especially appreciate the coordinating efforts of Dr. V. Gotceitas, S. Fraser, J. Linehan, M. Thistle, M. Ryan, Dr. C. Morris, B. Newton and K. Dalley. We offer special thanks to B. Newton for data support.

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Chapter 4 – Condition, size, and winter duration affect winter survival probability in juvenile Atlantic cod (*Gadus morhua*) in a coastal subarctic ecosystem

A version of this chapter was submitted for publication as: Geissinger, E. A., Bloom, C. R., Gregory, R. S., Laurel, B. J., and Snelgrove, P. V. R. Condition, size, and winter duration affect winter survival probability in juvenile Atlantic cod (*Gadus morhua*) in a coastal subarctic ecosystem. Marine Ecology Progress Series, *in review*.

4.1 Abstract

Juvenile Atlantic cod (*Gadus morhua*) in coastal Newfoundland settle in nearshore habitats in 3-6 pulsed events each year, creating a broad size-structured age-0 within each year-class with potentially different survival trajectories entering their first winter. We hypothesized that early arriving pulses, high fall body condition, and low winter severity would contribute to high first winter survival of age-0 juvenile cod. To test these hypotheses, we examined juvenile cod catch data, archived samples, and winter temperature records to determine the impact of winter duration, body condition, and settlement time on winter survival from 2001-2019. Late-arriving pulses of fish were small-sized before winter onset, but these pulses unexpectedly survived better than pulses settling earlier in the fall. However, all pulses had a survival advantage when settlement occurred earlier on average (associated with warmer falls) than later in the fall, suggesting increased growth and size within a pulse can also contribute to overwintering success. Fish condition did not vary across pulses within a given year-class, but we observed higher survival in years where fish were in better pre-winter condition. In contrast, higher survival occurred in years where remaining fish were in lower post-winter condition, which suggests limited foraging opportunities during winter. Effects of winter duration on survival were less than expected. Our findings challenge some assumptions of overwintering ecology (e.g., 'bigger is better', low

temperature stress) but illustrate the importance of cohort effects for overwinter survival in a sub-arctic marine ecosystem in a changing climate.

4.2 Introduction

Recruitment dynamics play an important role in fisheries management, and previous studies have hypothesized that in marine fishes, recruitment patterns are largely set in the larval stage (Hjört, 1926; Bannister *et al.*, 1974; Oeberst *et al.*, 2009). Many challenges constrain efforts to determine biological and physical drivers that predict cohort strength from data collected at the earliest life stages; yet interactions between biological and physical drivers demonstrate the importance of evaluating survival across multiple early-life stages (Ottersen and Loeng, 2000; Ottersen *et al.*, 2014). Pre-recruit abundances and cohort strength vary across species, time, and populations, and older pre-recruits (age-0 juveniles) can provide an early indication of adult recruitment for fisheries management (Stige *et al.*, 2013). Juvenile abundance has been linked to cohort strength in several fish species (Atlantic salmon *Salmo salar*, Niemelä *et al.*, 2005; haddock *Melanogrammus aeglefinus*, Stige *et al.*, 2019; Atlantic cod *Gadus morhua*, Lunzmann-Cooke *et al.*, 2021), demonstrating the importance of juvenile abundance as an indicator of future population status in marine fish species. However, age-0 juvenile recruitment signals may 'disappear' in sub-arctic/arctic fish populations by way of high overwintering mortality (Laurel *et al.*, 2017), indicating the need to account for regional environmental and biological factors later in the juvenile phase (Churchill *et al.*, 2011; Stige *et al.*, 2013).

Individual size among juveniles strongly influences overwinter survival in lakes (Post and Evans, 1989), with increased survival in larger compared to smaller individuals (Byström *et al.*, 2006; Huss *et al.*, 2008). Differences in survival may be size-dependent, reflecting higher weight-specific standard metabolic rates and lower energy storage in smaller individuals, leading to depleted energy reserves throughout winter (Paloheimo and Dickie, 1966; Shuter and Post, 1990; Lankford and Targett, 2001). However, winter energy depletion may be less of a concern in Arctic regions where fish can both feed and maintain body condition throughout winter, even with only modest food availability (Geissinger *et al.*, 2021). Yet, in the complete absence of food, high overwinter mortality likely occurs across a range of winter environmental conditions, with smaller juveniles more susceptible to earlier starvation than larger conspecifics (Post and Evans, 1989; Geissinger *et al.*, 2021).

Pre-winter size variation within an age-0 juvenile cohort can occur by way of several mechanisms including spawning timing (Conover *et al.*, 2003), selective mortality (Sogard, 1997), and growth (Dolan *et al.*, 2021), and can become magnified in demersal species when pelagic-demersal transitions (‘settlement’) are not synchronized in time and space. Multiple settlement ‘pulses’ occur in numerous flatfish species (e.g., winter flounder *Pseudopleuronectes americanus*, Sogard and Able, 1992; European plaice *Pleuronectes platessa*, Geffen *et al.*, 2011), when flatfish metamorphose and settle to the benthos, which in turn affects post-settlement growth and mortality rates (Geffen *et al.*, 2011). Atlantic cod in Newfoundland may be an extreme example, where as many as six settlement pulses occur throughout the summer and into the late fall (Methven and Bajdik, 1994; Grant and Brown, 1998; Gregory *et al.*, 2019). These settlement pulses likely result from protracted spawning, but link to onshore wind events that occur within three days of juvenile fish arriving to the nearshore (Ings *et al.*, 2008). Settlement pulses in Atlantic cod produce distinct size classes (Methven and Bajdik, 1994; Ings *et al.*, 2008), which can be identified with length frequency histograms and mixture distribution models (Chapter 3). This pattern contrasts plaice, which settle in two to three pulses associated with spring tides (Geffen *et al.*, 2011) and winter flounder, which settle in only two pulses associated with spawning within estuaries (Pearcy, 1976; Dolan *et al.*, 2021).

The absence of winter field observations has limited our understanding of overwintering dynamics in marine fish. However, snapshots in the fall and spring provide an opportunity to study winter ecology based on the demographics of the population during these two time periods. To determine the influence of cohort demographics on 1st winter survival of Newfoundland coastal cod, we used data and archived samples from a long-term monitoring program where settlement pulses of juvenile cod were annually tracked from July to the following spring from 2001 to 2019 (Chapter 3; Gregory *et al.*, 2019). In addition to settlement timing, we considered associations of winter duration, fish condition (pre- and post-winter), and size class (represented by recruitment pulse) on winter survival within each year. We hypothesized: (H1) long, cold winters, as defined by number of days below 1 °C, decrease survival of the smallest size class of age-0 Atlantic cod, (H2) higher survivorship characterizes age-0 cod with high body condition entering long, cold winters compared to age-0 cod with low body condition, and (H3) higher survival occurs in age-0 cod with high or sustained body condition after winter.

4.3 Methods

4.3.1 Study site, fish sampling, and water temperature:

Newman Sound is a fjord of Bonavista Bay, Newfoundland located adjacent to Terra Nova National Park. We used a seine net to capture juvenile fishes at 12 shore sites in Newman Sound (Fig. 4.1) every two weeks from July to November, and one week in May, from 2001 to 2019. The seine net was approximately 25 m long and 2 m high, consisting of 9 mm stretched mesh. The net was deployed 55 m from the shore from a small open boat and retrieved by two individuals standing 16 m apart. The seine samples approximately 880 m^2 of seabed habitat from the seabed to 2 m into the water column with a capture efficiency of approximately 95% (Gotceitas *et al.*, 1997). Age-0 and age-1 Atlantic cod were captured, counted, measured (to the nearest mm SL, standard length, from the tip of the snout to the end of the caudal peduncle) and returned live to the site of capture. A maximum of 10 Atlantic cod were haphazardly collected, euthanized, and preserved in 4% formalin in seawater during each sampling trip; individuals were then transferred to 95% ethanol within 48 hours for long-term storage.

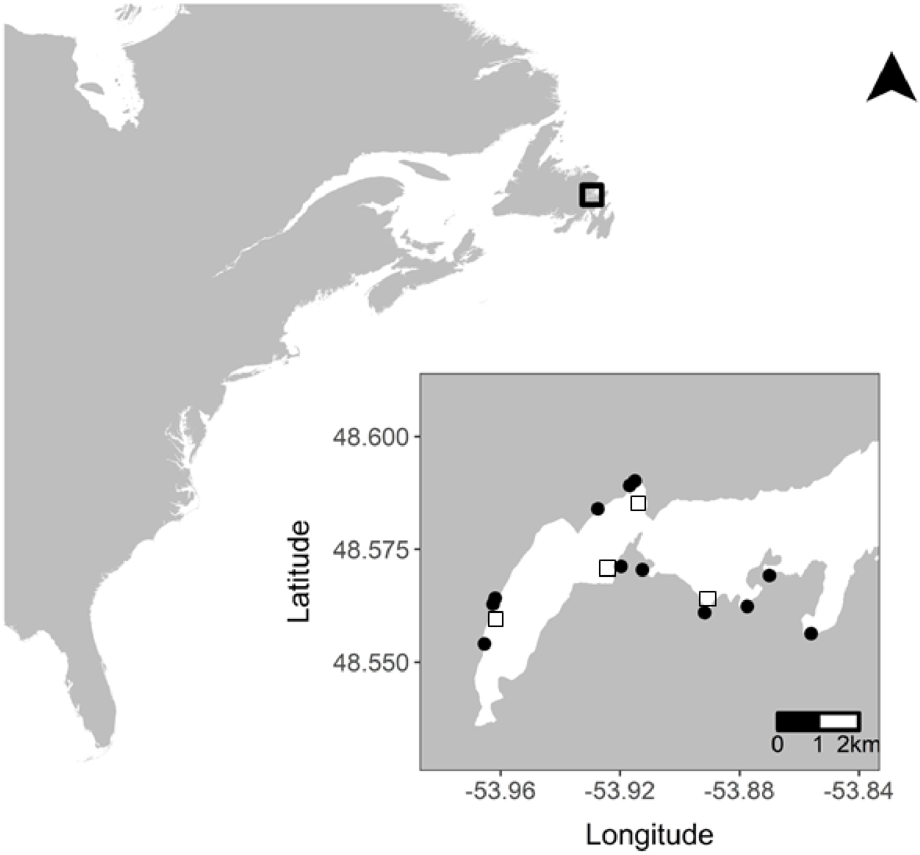

Figure 4.1. Map of 12 sites in Newman Sound, Newfoundland, Canada. Juvenile Atlantic cod (*Gadus morhua*) were sampled by a boat-deployed beach seine from 2001-2019 during May and July to November. Open squares represent locations of Minilog-T-II thermographs (™Vemco Ltd.), placed 25 cm above the ocean floor at an approximate water depth of 3 m.

We obtained hourly temperature using Minilog-T-II thermographs (™Vemco Ltd.) placed in four locations in Newman Sound at 25 cm above the ocean floor at a water depth of approximately 3 m; we have expressed these data as mean daily temperature. We defined start of winter for each year as the date when mean daily temperature fell below 1 °C, and end of winter as the date when mean daily temperature exceeded 1 °C, for at least three consecutive days. We calculated average winter temperature and standard deviation for the periods between start and end dates of winter each year, and length of winters as the number of days during the winter period with mean daily temperatures below 1 °C.

4.3.2 Statistical analysis:

We calculated fish abundance as mean number of age-0 juvenile Atlantic cod caught per seine haul for each sampling period across all 12 sampling sites, and then grouped them by settlement pulse. We selected October as our pre-winter sampling period for each year because it represents a reliable abundance estimate before juveniles move to deeper water; similarly, we selected July of the following year as the post-winter sampling period because July represents a reliable post-winter estimate of abundance when nearshore waters are cool, and age-1 fish are available to the seine (R. Gregory, unpubl. data). Pre-winter and post-winter abundance were used to estimate winter survival probability. Sampling constraints and availability of fish in the sampling zone limited sampling to periods approximately 9 months apart. Juvenile fish become less abundant in November when temperatures begin to drop (Methven and Bajdik, 1994), therefore limiting our ability to draw inference on abundance estimates past October. Winter (<1 °C) ranges from 2-6 months, with the earliest start date in mid-December, and latest end date in mid-June.

We used finite mixture distribution models (Macdonald and Du, 2018) to determine the size-class distributions for each sampling trip, and assigned the pulses based on growth trajectories over the course of the season (Chapter 3; Gregory *et al.*, 2019) through visual inspection of scatter plots and histograms. This process allowed us to assign settlement pulses at both age-0 stages in the fall and again at age-1 stages the following spring. Settlement date was estimated by regressing daily modal length against Julian date and daily temperature (°C) to account for temperature-dependent growth and back calculated to the date using an initial settlement size of 39 mm SL (Ings *et al.*, 2008).

All preserved fish were blotted dry, weighed to ±0.01 g and ±1 mm SL. Fulton's condition factor, K, was calculated as:

$$K = 100 \cdot (W \cdot L^{-3}), \qquad (1)$$

with W as weight (g) and L as standard length (cm SL; Fulton, 1904). Fulton's K is an imprecise measure of energy but can serve as a relative measure of fish condition (Lambert and Dutil, 1997; Grant and Brown, 1999).

We evaluated fish abundance by cohort (i.e., year-class), and calculated average abundance and condition, both pre-winter and post-winter, and the length of winter for Pulse 1 (P1), Pulse 2 (P2), Pulse 3 (P3), and Pulse 4 (P4) for 18 cohorts 2001 – 2018. Only two pulses (P2 and P3) had sufficient data to include in the full model using all explanatory variables (pre- and post-winter abundance, pre- and post-winter condition). Our analysis also excluded individuals settling after October because of limited archived samples in November. Analysis of survival probability (post-winter abundance/pre-winter abundance) used a generalized linear model in R with a binomial error distribution and logit link (logistic ANCOVA). We assessed the model fit using visual residual diagnostics, McFadden's Pseudo R^2 (Veall and Zimmerman, 1994), and likelihood ratio (LR). Analysis of Deviance (ANODEV) was used to evaluate the significance of explanatory variables. We calculated effect size of explanatory variables (survival odds) using odds:

$$\text{Odds}= e^{\beta_I}, \tag{2}$$

with β_i as the coefficient estimate with the logit link. Survival odds are expressed as odds ratio. Calculations of predictor effects for generalized linear models used the *effects* package in R (Fox, 2003; Fox and Hong, 2009; Fox and Weisberg, 2018, 2019).

Relationships between several variables were investigated in subsequent models due to the limited degrees of freedom for their inclusion in the full model. Where possible, Pulse 1 and Pulse 4 were included in analyses. Interactive effects were only included if $p < 0.05$. Annual variation in pre-winter K and post-winter K was assessed using a general linear model (GLM) with a Gamma distribution and log link. Pre-winter K (P1, P2, P3) and post-winter K (P2, P3, P4) were response variables in separate models, and cohort was included as a categorical explanatory variable. The effects of pulse, settlement time, and winter duration on post-winter K (P2, P3) were assessed with the following generalized linear models (GLMs): post-winter K (response) in relation to pulse (categorical) and settlement week (continuous); post-winter K (response) in relation to pulse (categorical) and winter duration (continuous). Both models used a Gamma distribution with log link.

The relationship between post-winter K (response) and pre-winter K (explanatory) was assessed using a GLM with Gamma distribution and log link (P2 and P3). Additional relationships between pre-winter K (response) and the following explanatory variables were assessed in individual GLMs: pulse, mean standard length (SL), settlement week, and mean October temperature (P1, P2, P3).

Statistical models were conducted in R using *car* (Fox and Weisberg, 2019). All data organization and data visualization were conducted in R using *tidyverse* (Wickham *et al.*, 2019; R Core Team, 2021).

4.4 Results

4.4.1 Data summary

From 2001 to 2018, the earliest settlement time for Pulse 1 (P1) occurred in 2006. Earliest settlement time for Pulse 2 (P2), Pulse 3 (P3), and Pulse 4 (P4) occurred in 2008. The latest settlement time occurred in 2002 for Pulse 1, Pulse 2, and Pulse 3, with the latest settlement time for Pulse 4 occurring in 2010. Pulse 1 settlement time ranged from early-July to late August, with an October mean length of 76.6 ± 10.0 mm SL (smallest length 2002 67.0 ± 9.4, largest 2004 118.0 ± 4.2 mm SL). Pulse 2 settlement time ranged from mid-August to early October, with an October mean length of 59.3 ± 7.4 mm SL (smallest length 2012 55.5 ± 7.3, largest 2006 76.0 ± 16.2 mm SL). Pulse 3 settlement time ranged from early September to mid-November, with an October mean length of 47.6 ± 7.9 mm SL (smallest length 2005 35.6 ± 6.9, largest 2008 60.8 ± 5.1 mm SL). Pulse 4 settlement time ranged from early October to early December. Average settlement time between recruitment pulses was 4.9 ± 1.4 weeks. The shortest interval between recruitment pulses was 2 weeks (between P1 and P2 in 2017), and the longest interval between recruitment pulses was 8 weeks (between P1 and P2 in 2006; P2 and P3 in 1998 and 2007).

Condition (K) for Pulse 1, 2, and 3 entering winter ranged from 0.51 - 1.1 (Fig 4.2a). Pre-winter Fulton's K varied significantly by cohort ($\chi^2 = 394.8$; df = 16,510; $p < 0.0001$). However, we detected no significant difference in pre-winter Fulton's K between pulses within each cohort ($p > 0.05$). Pre-winter K for the entire time-series averaged 0.71 ± 0.08. Mean Fulton's K was lowest in the 2017 cohort (0.59 ± 0.06) and highest in the 2012 cohort (0.84 ± 0.08).

Condition for Pulse 2, 3, and 4 after winter ranged from 0.48 - 1.0 (Fig. 4.2b). Post-winter Fulton's K varied significantly by cohort ($\chi^2 = 127.5$; df = 15,270; $p < 0.0001$). Post-winter K for the entire time-series averaged 0.70 ± 0.09, with the lowest mean Fulton's K (0.62 ± 0.05) for the 2005 cohort and highest mean Fulton's K (0.85 ± 0.05) for the 2016 cohort.

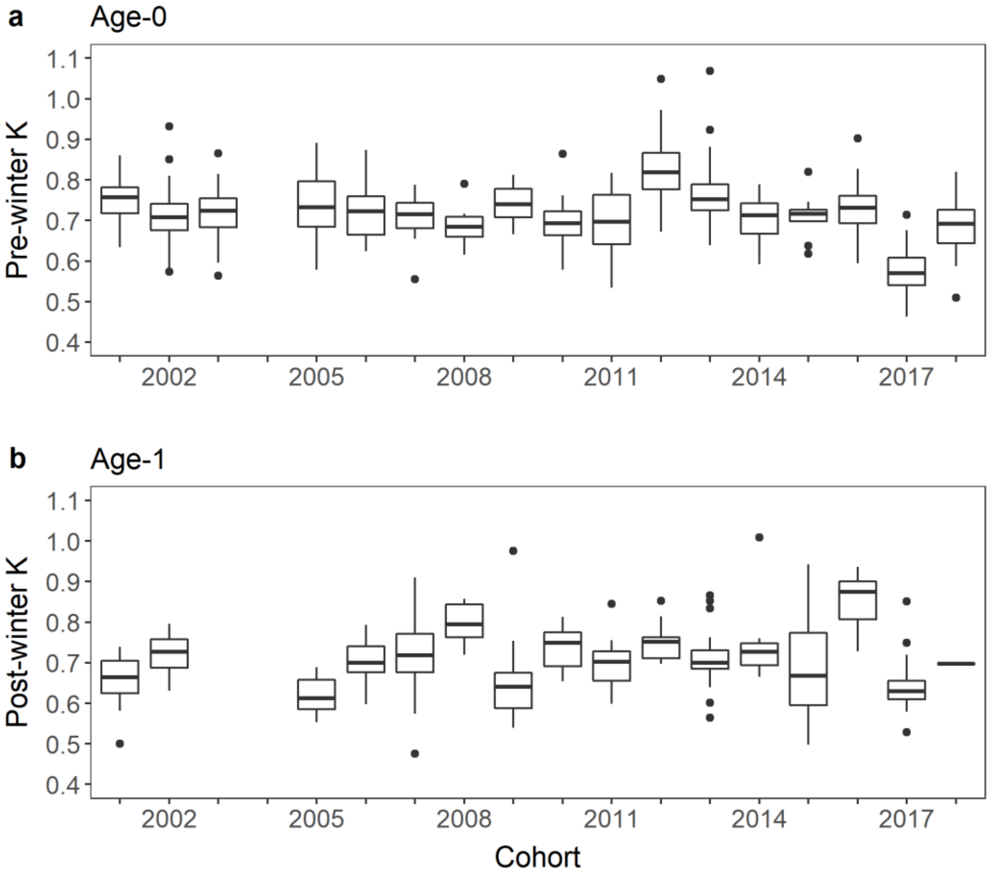

Figure 4.2. Fulton's K condition factor of age-0 *Gadus morhua* for (a) October (pre-winter) and (b) May (post-winter) for each annual cohort from 2001 to 2018. The bold line represents the median of all sampled juveniles for each cohort, the lower and upper hinges correspond to the first and third quartiles, and the

upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Individual points represent outliers.

The 2007 cohort experienced the longest winter duration at 131 days (~4 months) – with an average winter temperature of -0.15 ± 0.56 °C, whereas the 2010 cohort experienced the shortest winter – 64 days (~2 months) – with an average winter mean temperature of 0.47 ± 0.36 °C. The 2010 cohort also experienced the mildest winter among all years in this study, whereas the 2015 cohort experienced the coldest, with a mean temperature of -0.44 ± 0.39 °C and 110 days below 1 °C (Fig. 4.3).

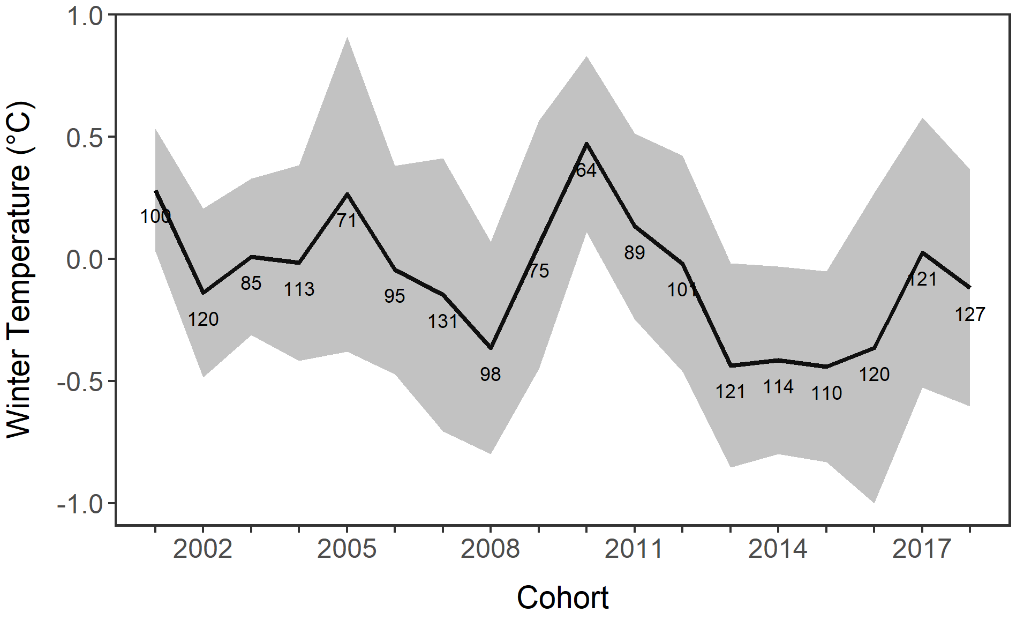

Figure 4.3. Mean winter temperature (°C) in Newman Sound, Newfoundland for each cohort (2001-2018) Grey shading represents ± standard deviation. Numbers represent the number of days below 1 °C for each winter.

4.4.2 Model results

A single outlier was removed in our analysis based on Cook's Distance measure (i.e., 2016 P2). The full model, which included Pulse 2 and Pulse 3, yielded a Pseudo R^2 of 0.988 (LR = $2.85 \cdot 10^{17}$). Analysis of deviance (ANODEV) showed that all explanatory variables explained significant variance in survival probability (Table 4.1).

Table 4.1. Type-III Analysis of Deviance of the effect of pulse, pre-winter condition, post-winter condition, and Days Below 1° C on survival probability of age 0 *Gadus morhua* from the 2001-2018 cohorts from Newman Sound, Newfoundland. Data modeled with a generalized linear mixed effect model, with cohort as the random effect, using a binomial error distribution and logit link. Residual deviance was 24.8 on 14 degrees of freedom.

Source	**DF**	**LR Chi-Square**	**Pr > ChiSq**
Pulse	1	34.1	$5.24 \cdot 10^{-9}$
Settlement week	1	4.94	0.0262
Pre-winter K	1	33.1	$8.78 \cdot 10^{-9}$
Post-winter K	1	7.71	0.00549
Days Below 1 °C	1	10.4	0.00129

Pulse influenced survival probability; Pulse 3 had a 47:1 odds ratio (OR) relative to Pulse 2. Survival probability increased from 0.01 (0.00036 – 0.036) in Pulse 2 to 0.35 (0.22 – 0.50) in Pulse 3 (Fig. 4.4a). Settlement week for Pulse 2 and Pulse 3 was significantly associated with survival probability; survival odds decreased by 56% (OR = 0.44:1) when pulses settled later in the season. Survival probability decreased from 0.34 (0.11 – 0.67) when settling early in the season to 0.015 (0.0020 – 0.10) when settling late in the season, approximately 11 weeks apart (Fig. 4.4b).

Pre-winter K was also significantly associated survival probability, with a 6.2:1 OR, Survival probability increased from 0.0032 (95% CI: 0.00055 – 0.017) when prewinter K was 0.58 to 0.74 (0.43 – 0.91) when pre-winter K was 0.85 (Fig. 4.4c). Post-winter K was significantly associated with survival probability; survival odds decreased by 75% (OR = 0.30:1) with increased post-winter K. Survival probability decreased from 0.58 (0.15 – 0.92) when post-winter K was 0.59 to 0.021 (0.0052 – 0.079) when post-winter K was 0.76 (Fig. 4.4d).

Winter duration had a small effect on survival probability, with a 2.0:1 change in survival odds with increase in winter duration. Despite the limited impact of winter duration, our model predicted increased survival probability during longer winters, with a survival probability of 0.0096 (0.0014 – 0.063) when 64 days fell below 1° C, and a survival probability of 0.33 (0.18 – 0.53) when 131 days fell below 1° C (Fig. 4.4e).

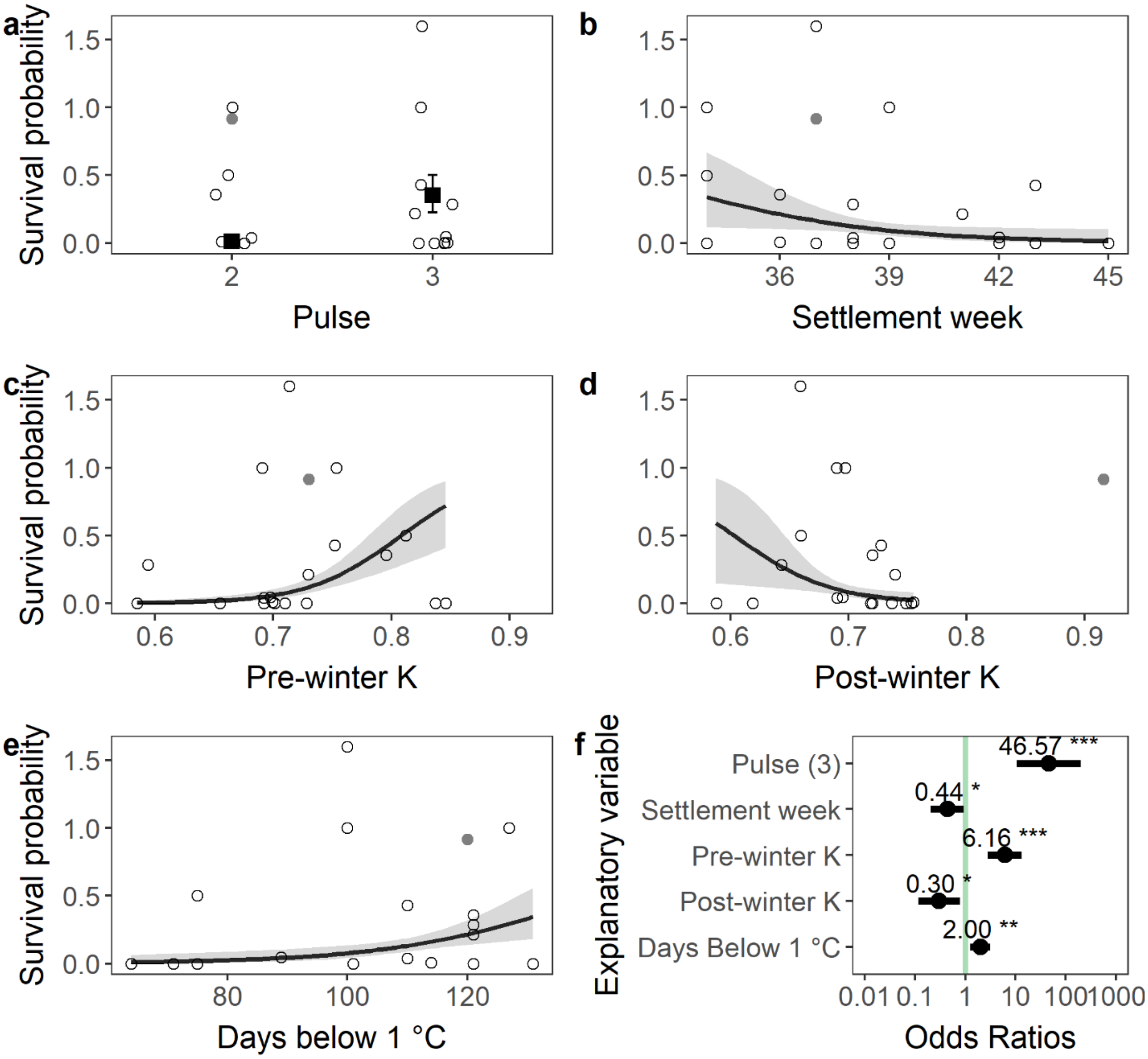

Figure 4.4. Predictor effects for survival probability of age-0 *Gadus morhua* for Pulse 2 and Pulse 3 from 2001 to 2018. The effect of (a) pulse, (b) settlement time, (c) pre-winter Fulton's K, (d) post-winter Fulton's K, and (e) days below 1 °C on survival probability is shown as the back-calculated estimates from a generalized linear model with a Gamma distribution and log link. The effect of pulse structure (a) on survival probability is indicated by black squares. The effect of pre-winter Fulton's K (b), days below 1 °C (c), and post-winter Fulton's K (d) on survival probability are indicated by the regression line, back-transformed from a log link. Open circles are individual data points. Error bar (a) and grey shading (b, c, d) represent 95% confidence intervals (CI). The grey solid point represents data from an outlier year (2016, pulse 2), which was not included in the generalized linear model. Model output with (f) Odds Ratios for each explanatory variable; asterisks indicate statistical significance ($p < 0.05$).

4.4.3 Settlement timing

Warmer fall temperatures were associated with earlier settlement within each pulse (P1, P2, P3, P4) in a given year ($\chi^2 = 15.4$; df = 1,58; $p < 0.001$; Fig. 4.5). Based on the model, settlement occurred one week earlier for every 1.2 °C increase in temperature in the fall. The greatest difference in settlement timing occurred between year 2008 (12.4 ± 2.2 °C) and 2002 (10.7 °C) where there was a 4-week difference in settlement timing in Pulse 1, and a 7- to 10-week difference in settlement timing among the remaining pulses.

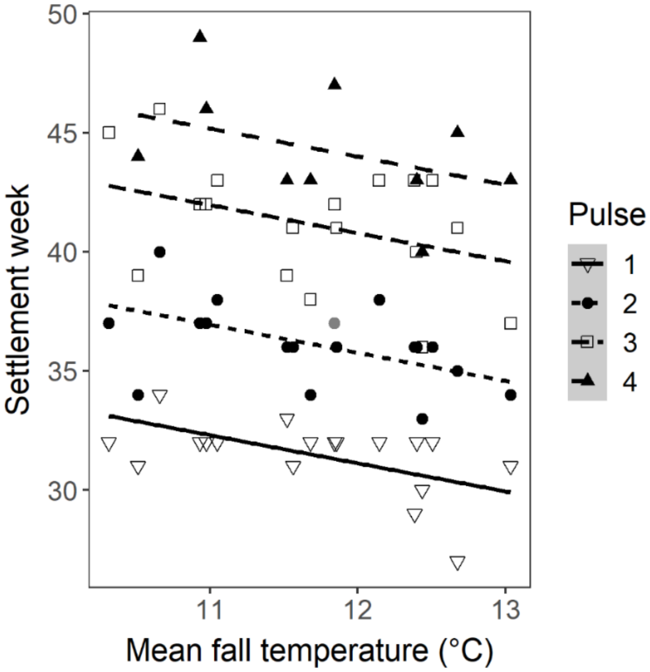

Figure 4.5. Settlement week estimates for age-0 *Gadus morhua* in the 2001-2018 cohorts from Newman Sound, Newfoundland across mean fall temperatures (°C). Estimates are produced from a general linear model with pulse as a categorical variable and fall temperature as a covariate. Change in settlement week was associated with fall temperature for Pulse 1, 2, 3, and 4. Regression lines estimated from a Gaussian distribution. Individual points represent post-winter Fulton's K measurements for Pulse 1 (inverted triangle), Pulse 2 (circle), Pulse 3 (square), and Pulse 4 (triangle). Pulse 2 from the 2016 cohort is denoted in grey.

4.4.4 Condition

As expected, juvenile cod were in lower condition following the winter period, but cohorts starting with higher pre-winter condition tended to be in higher post-winter condition ($\chi^2 = 5.16$; df = 1,6; p = 0.023). A 0.10 increase in mean pre-winter K condition values resulted in a 0.07 increase in mean post-winter K condition values (Fig. 4.6). Pulse (P1, P2, P3), mean length, settlement week, and fall temperature did not affect pre-winter condition ($p > 0.40$).

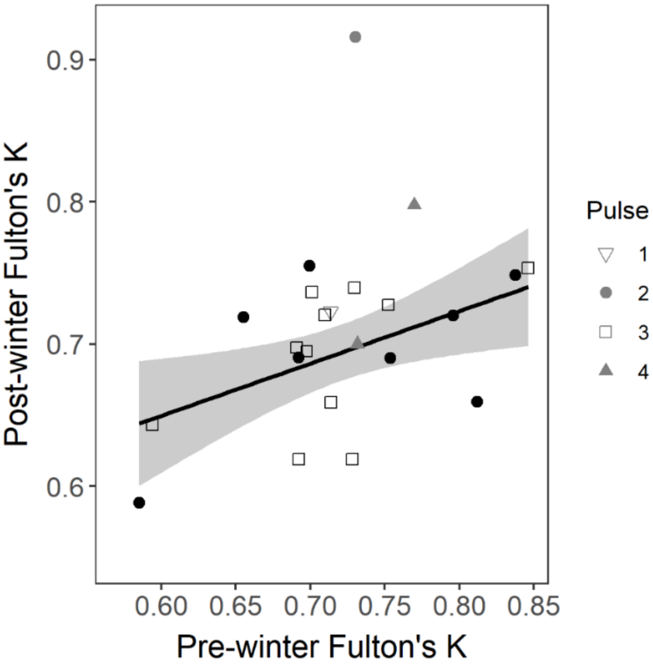

Figure 4.6. The relationship between post-winter Fulton's K and pre-winter Fulton's K for age-0 *Gadus morhua* in the 2001-2018 cohorts from Newman Sound, Newfoundland. Change in post-winter Fulton's K based pre-winter Fulton's K for Pulse 2 and 3 are shown by the regression lines. Regression lines are back-transformed estimates from a Gamma distribution and log link with pulse as a categorical variable, and pre-winter K as a covariate. Gray shading represents 95% confidence intervals (CI). Individual points represent post-winter Fulton's K measurements for Pulse 1 (inverted triangle), Pulse 2 (circle), Pulse 3 (square), and Pulse 4 (triangle). Grey points represent data that were not included in the model, and the grey circle represents data from the outlier year (2016 cohort).

Post-winter K (P2, P3, P4) did not vary by pulse or settlement time when variables were included in separate models ($p > 0.5$). However, change post-winter K was associated with pulse and settlement time (Pulse: $\chi^2 = 4.59$; df = 1,16; $p = 0.032$; Settlement time: $\chi^2 = 6.62$; df = 1,16; $p = 0.010$) when the two variables were included together as an analysis of covariance (ANCOVA). Pulse 2 and 3 had higher mean post-winter K by ~0.14 when they settled 11 weeks later in the season. On average, Pulse 2 had higher post-winter K (K = 0.73, CI: 0.68 – 0.78) compared to Pulse 3 (K = 0.66, CI: 0.63 – 0.70; Fig. 4.7). Winter duration had no effect on post-winter K ($p > 0.05$).

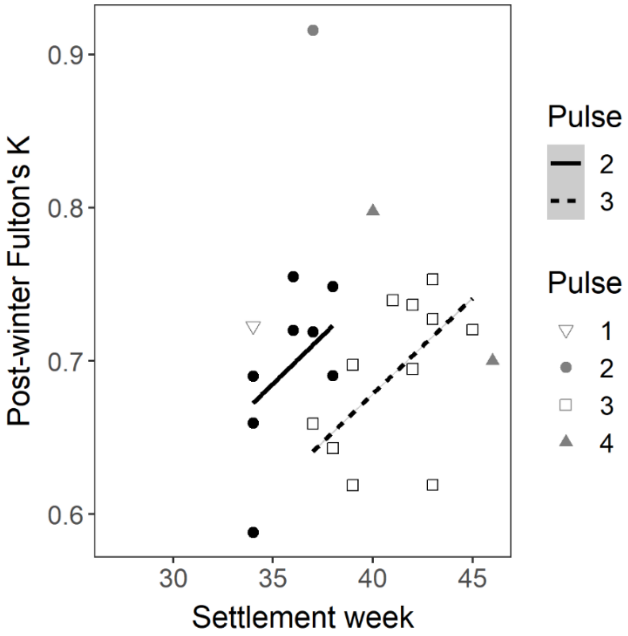

Figure 4.7. Post-winter Fulton's K by settlement week for age-0 *Gadus morhua* in the 2001-2018 cohorts from Newman Sound, Newfoundland. Change in post-winter Fulton's K based on settlement week for Pulse 2 and 3 are shown by the regression lines. Regression lines are back-transformed estimates from a Gamma distribution and log link with pulse as a categorical variable, and settlement week as a covariate. Gray shading represents 95% confidence intervals (CI). Individual points represent post-winter Fulton's K measurements for Pulse 1 (inverted triangle), Pulse 2 (circle), Pulse 3 (square), and Pulse 4 (triangle). Grey points represent data that were not included in the model, and the grey circle represents data from the outlier year.

4.5 Discussion

The challenges of winter sampling have limited the characterization of overwinter survival in marine systems (Hurst, 2007), but our long-term field dataset from the pre- and post- winter period reveals that multiple factors influence survival probability of juvenile Atlantic cod in their first winter. A priori, we expected higher age-1 survivorship among age-0 cod entering winter with better body condition and at a larger size (resulting from early pre-winter settlement) compared to juveniles in poorer condition and at a smaller size (resulting from later pre-winter settlement). Similarly, we expected higher survival for cohorts experiencing mild annual winter conditions than those experiencing harsher winters (longer, colder). Our results show that: 1) winter duration had a limited effect on survival and small body size was unexpectedly associated with higher winter survival (based on settlement timing; rejection of H1), 2) high pre-winter body condition increased survival probability (support for H2), but 3) highest post-winter body condition was associated with low survival years (rejection of H3). These results challenge several assumptions of overwinter ecology (e.g., 'bigger is better', low temperature stress) but emphasize the importance of settlement timing and fish condition on future survival. We discuss these results below in the context of current and future climate scenarios.

4.5.1 Size and settlement timing

Settlement timing and pulse structure significantly influenced winter survival probability. Despite clear evidence that higher survivorship occurs in large juveniles of most fishes (Werner and Gilliam, 1984; Moss *et al.*, 2005; Hurst, 2007), we observed highest survival probability in our smallest (late pulse) groups of juveniles. This finding was surprising given the increased ability of larger age-0 cod to survive low-food scenarios during winter (Geissinger *et al.*, 2021) and general ability of larger fish to evade predators (Van der Veer *et al.*, 1997; Lundvall *et al.*, 1999;

Cowan, 2002). Despite no statistical difference in pre-winter body condition among pulses, there could be energetic differences among recruitment pulses in variables such as lipid content that Fulton's K could not detect. Our results were unanticipated based on energetic principles and processes, suggesting a need for further research on energy content of recruitment pulses entering winter. Predation might also explain the size-structured survival observed in our study. Potentially, late pulse fish face lower predation pressure because of fewer predators during their settlement time. A time- or size-dependent predator window may explain the high survival probability of smaller-sized late pulse juveniles by way of several potential mechanisms. For example, late pulse fish settle into nearshore structured habitats (e.g., eelgrass, kelp) after predators move into deeper waters in the fall, thereby significantly reducing predation rates (Linehan *et al.*, 2001; MacRobert, 2020). Alternatively, energy reserves could differ in later pulses that retain reserves from their pelagic phase, which help them survive winter (*sensu* Copeman *et al.*, 2008).

We were unable to assess the survival probability of the first settlement pulse (early August) accurately because low abundances or complete absence of the first settlement pulse often occurred in the nearshore during our late fall (as age 0) and spring (as age 1) sampling period (e.g., Gregory *et al.*, 2019). We were also unable to assess the survival probability of the fourth settlement pulse (late November) accurately because of low abundances or complete absence of the fourth pulse during fall sampling.

Settlement timing within a pulse also influenced survival probability, with a survival disadvantage for late settlement within a given year. Settlement timing for all pulses shifted earlier under warmer fall conditions, which may simply represent faster pre-settlement growth and earlier settlement competency (Dolan *et al.*, 2021). However, waves dominate circulation within Newfoundland inlets (Syvitski *et al.*, 1987), and coastal winds resulting in downwelling events link with timing of settlement and nearshore temperature for age 0-cod (Ings *et al.*, 2008). The physical oceanography of the coastal system in the late summer-early fall period (temperature, downwelling events) may therefore structure biological processes for juvenile cod both immediately (settlement timing and condition) and into the following year (overwintering success). Delineating the contrasting advantages between early settlement versus late settlement pulse will require further research. Studies on settlement time at a coarser scale can help determine if either settlement time or size entering winter drive winter survival. Additionally, a better understanding of energetic benefits for early vs. late settlement and predator windows will improve our understanding of this complex and counter-intuitive result.

4.5.2 Pre-winter condition

High pre-winter condition resulted in high overwinter survival, which is consistent with other studies on high-latitude fish species (Heintz *et al.*, 2013; Sewall *et al.*, 2019). In our study, condition did not vary among pulses within cohorts, indicating similar rates of increase in weight/body length ratios annually among recruitment pulses. Potentially, once cod settle (regardless of pulse), they switch to a growth allocation strategy leading to increased length, presumably to avoid predation (Post and Parkinson, 2001; Copeman *et al.*, 2008; Siddon *et al.*, 2013). Juvenile fish often use one of two alternative strategies: (1) maximize somatic growth or (2) maximize lipid storage (Post and Parkinson, 2001). Energy allocation strategies in Arctic gadid species (e.g., Polar cod, *Boreogadus saida*, and Saffron cod, *Eleginus gracilis*) under laboratory conditions appear to favor energy storage over growth as temperatures decline in the fall (Copeman *et al.*, 2016), presumably because more energy can be allocated to fat in Atlantic cod as metabolic demands decrease with temperature (Jobling, 1995). Despite this pattern, increased condition may be associated with higher temperatures in coastal nurseries e.g., Pacific cod (*Gadus* *macrocephalus*, Abookire *et al.*, 2022). In our study, pre-winter condition was relatively consistent across pulses and thermal conditions within a given year, although we acknowledge that wet Fulton's K may be too coarse of a condition metric to detect modest differences in annual fall temperature.

4.5.3 Post-winter condition

Surprisingly, post-winter condition was highest during low survivorship years. Condition post-winter can indicate whether fish needed to use their energy stores (low food) or were able to maintain or improve their energy reserves (high food). Condition loss throughout winter typically results from low food availability, in worst years leading to their death (Geissinger *et al.*, 2021). In the absence of food, juvenile roach (*Rutilus rutilus*) condition decreases at a faster rate during warm winters than cold winters (Brodersen *et al.*, 2011). In contrast, juvenile Atlantic cod can increase their body condition at temperatures ranging from -0.7 to 2.5 °C when food is available even in small quantities (Geissinger *et al.*, 2021). Across most years, juvenile cod were in poorer condition after winter, suggesting very limited winter foraging opportunities for juvenile cod in coastal Newfoundland. Interestingly, winter duration had no effect on post-winter condition. These results highlight that juvenile cod are well suited to cold temperatures. However, they are still susceptible to metabolic (energy storage) and behavioral (foraging) stressors in winter environments.

We showed that settlement time also explained variance in post-winter condition, highlighting the complexity of a multi-pulsed population. We interpret our findings as evidence of a tradeoff to settling later in the season. Pulse 2 and Pulse 3 had higher post-winter condition when settling later in the season, but experienced lower survival probability. Food quality and availability may differ throughout the fall season and could explain observed differences in post-winter condition based on settlement time. Although Fulton's K can detect total available energy reserves in cod (Lambert and Dutil, 1997), it offers limited information on types of energy reserves available. Fulton's K provides no direct information on food quality or the total available energy between pulses or settlement times. However, lipid class and fatty acid composition change when juvenile cod transition from pelagic to demersal prey types following settlement (Copeman *et al.*, 2008). Evaluating multi-pulse diet and energetics within coastal Newfoundland Atlantic cod is beyond the scope of our study and would require finer temporal measurement of fall growth and energy allocation.

4.5.4 Winter duration

The benefit of longer winters on overwintering survival was an unexpected result. In laboratory settings, juvenile cod can maintain growth under low food environments under cold conditions (<1 °C) for months at a time (Geissinger *et al.*, 2021). Winter thermal habitats may also exclude predators in nearshore ecosystems (Kristiansen *et al.*, 2001). For example, tagging studies indicate age-2 Greenland cod (*G. macrocephalus ogac*), a known predator on age-0 cod, move away from nearshore habitats in winter (Shapiera *et al.*, 2014). Noting the primary importance of high pre-winter condition for survival, juveniles likely depend on their winter fat reserves until spring, although high post-winter condition in some years suggests periodic winter foraging (this study; Geissinger *et al.*, 2022). Therefore, coastal cod in Newfoundland may require sufficiently long winters to reduce metabolic demand and predation risk during periods of low productivity.

One year stood out among our cohorts (2016), with high post-winter condition, and high survival probability. A concurrent tagging study in Newman Sound in 2016-2017 provided further support for high survival in showing low winter mortality for age-0 cod (0.005 – 0.0025% d^{-1};

Geissinger *et al.*, 2022). The high survival in 2016 was not associated with any fall or winter temperature anomaly. Despite the 2016 cohort experiencing a cold (-0.3) and moderately long (120 day) winter, it fell within the 1st quartile for mean temperature and days below 1 °C, indicating that 2016 was not an extreme year for juvenile cod. Therefore, the 2016 cohort may have represented a "goldilocks" zone of moderate physical and biological conditions for high winter survival.

4.6. Conclusions

We showed that large body size does not necessarily favor overwintering survival in juvenile Atlantic cod, and smaller individuals (i.e., later settlement pulses) can have a high survival probability. Additionally, healthy fish in the spring (high post-winter condition) does not necessarily indicate high winter survival had occurred. Smaller fish experiencing high survival contradicts most assumptions based on size. Smaller size entering winter may represent a trade-off with settlement time (including variation between and within pulses) and indicates a bet hedging strategy for Atlantic cod in Newfoundland coastal waters, allowing highest possible survivorship for at least one settlement pulse in a year noting the strong annual environmental variability typical of the Atlantic subarctic.

Fall temperatures may play an important role in survival trade-offs because: 1) survival probability decreased when recruitment pulses settled later in the season, and 2) warmer falls were associated with earlier settlement across all settlement pulses. Therefore, warm falls may promote high winter survival for all pulses settling earlier in the season, with an increased advantage for late pulses. However, warmer temperatures can also result in shorter, warmer winters, thereby decreasing survivorship. Our study did not fully explore these interactions, which will likely be important factors to consider under varying future climate scenarios.

Our study emphasizes the importance of characterizing age-0 Atlantic cod cohort demographics (size, condition) to assess survival in juvenile fish populations, and highlights the importance of seasonal sampling to assess multiple recruitment pulses. Simple metrics, such as Fulton's condition factor K, can complement size and abundance measures from surveys, and could be potentially further improved through energetic measures to improve predictions of survival probability to age-1. While acknowledging the complex dynamic pulse structure of coastal cod populations in Newfoundland, such variability in settlement time and pre-winter size may be an important component of historical and future climate resiliency in this population.

4.7 Acknowledgements

This research was sponsored by the Natural Sciences and Engineering Research Council of Canada through the NSERC (Canadian Healthy Oceans Network CHONe-I & II and two Strategic Projects grants), and its Partners: Department of Fisheries and Oceans Canada (including Productive Capacity, Environmental Science Strategic Research Fund, Atlantic Cod Science, Strategic Program for Ecosystem Research and Advice, Centre of Expertise for Aquatic Habitat Research; and Marine Conservation Targets programs) and INREST (representing the Port of Sept-Îles and City of Sept-Îles, Quebec), Environment Canada (Environmental Innovations Program - Green Plan), Parks Canada (Protected Areas Program; Species-at-Risk Fund), and Memorial University of Newfoundland. We thank over 250 MUN graduate and senior undergraduate students, DFO technical and biological support personnel, Parks Canada staff and other volunteers who contributed to this 25-year time series, and especially appreciate the coordinating efforts of K. Dalley, S. Fraser, Dr. V. Gotceitas, D. Lancaster, J. Linehan, Dr. C. Morris, B. Newton, M. Ryan, and M. Thistle. We offer special thanks B. Newton for data support and S. Anderson, J. Blundon,

C. Coombs, G. English, C. Fitzpatrick, J. Mack, A. Mersereau, T. Small, and K. Whittaker for lab support.

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Chapter 5 – Food and initial size influence overwinter survival and condition of a juvenile marine fish (age-0 Atlantic cod)

A version of this chapter was published as: Geissinger, E. A., Gregory, R. S., Laurel, B. J., and Snelgrove, P. V. R. 2021. Food and initial size influence overwinter survival and condition of a juvenile marine fish (age-0 Atlantic cod). Canadian Journal of Fisheries and Aquatic Sciences, 78: 462-482.

Data were published as: Geissinger, E. A., Gregory, R. S., Laurel, B. J., and Snelgrove, P. V. R. 2020. Data from: Food and initial size influence overwinter survival and condition of a juvenile marine fish (age-0 Atlantic cod). Available from https://doi.org/10.5683/SP2/8KUABH.

5.1 Abstract

In subarctic Newfoundland, age-0 Atlantic cod (*Gadus morhua*) settle into coastal habitats in several summer-autumn pulses, resulting in broad length-frequency distributions before winter. Low winter temperatures and potential decreases in food availability pose challenges for age-0 fish. To examine how size variation affects overwintering success under contrasting food scenarios, we conducted 114-day laboratory feeding trials at ambient overwinter sea temperatures, using demersal age-0 cod collected from Newman Sound, Newfoundland. We reared two size-classes of juvenile cod under four daily ration levels (starvation, low, medium, high). We used Fulton's K condition factor to interpret effects of food availability and fish size on survival overwinter. We showed that small amounts of consumed food ($<1\% \text{ BW} \cdot \text{d}^{-1}$) maximized winter growth and condition potential of juvenile cod in Newfoundland waters. With no food, survival of small cod dropped below 80% on Day 47, whereas survival of large juveniles remained >80% until Day 74. Therefore, we expect higher survival of earlier settlers and increased size-selective mortality in age-0 cod during either unproductive or protracted winters, when food abundance is often low.

5.2 Introduction

Juvenile fish experience high natural mortality in their first year of life (Sogard 1997; Kristiansen *et al.*, 2000). Despite multiple studies of mortality in juvenile Atlantic cod (*Gadus morhua*) during the summer and fall seasons (Lindholm *et al.*, 1999; Laurel *et al.*, 2003; Bogstad *et al.*, 2015) and several studies on population dynamics overwinter (Goddard *et al.*, 1992; Dutil and Lambert, 2000; Björnsson and Steinarsson, 2002), many aspects of overwinter survival remain unknown. In polar and temperate latitudes, low temperatures, and potential decreases in food availability in winter pose challenges for age-0 fish (Foy and Paul, 1999). Most information on overwinter dynamics in fish comes from freshwater systems with a particular focus on salmonids and centrarchids (e.g., Post and Evans, 1989; Pangle *et al.*, 2004; Mogensen and Post, 2012). While these studies provide a theoretical framework to examine overwintering processes in other species (e.g., size-dependent survival), marine systems require additional considerations given differences in cooling characteristics of the water column, scale (e.g., migration potential), and osmoregulatory stress (Hurst, 2007).

Current bioenergetic models to determine growth rates for fish often focus on spring, summer, and fall dynamics (Peck *et al.*, 2003; Mogensen and Post, 2012). However, sub-zero temperatures, size limitations, and food limitations expose juvenile fishes to different stressors and metabolic effects overwinter. General bioenergetic models generally lack parameters to assess overwinter dynamics, particularly given major knowledge gaps on survival and cold-water physiology of fish at sub-arctic temperatures. During winter, juvenile fish must cope with direct, indirect, and interactive effects of temperature decline with other environmental variables. Although temperature determines the underlying rate of energy store depletion (Pangle *et al.,* 2004; Huss *et al.*, 2008; Copeman *et al.*, 2017), extreme low temperatures can also cause acute thermal stress (Hurst, 2007), related to osmoregulatory function (Lankford and Targett, 2001) or freezing. Juvenile fish also experience size-dependent effects, with higher metabolic rates in smaller individuals (Werner and Gilliam, 1984; Byström *et al.*, 2006) and reduced capacity for lipid storage prior to winter (Huss *et al.*, 2008). The large ratio of gill surface area to body mass in small individuals may also increase juvenile vulnerability (Oikawa and Itazawa, 1985). However, superior acclimation capabilities in smaller individuals, such as more anti-freeze proteins than larger individuals (Fletcher *et al.*, 1987; Goddard *et al.*, 1992), may help offset these risks.

Growth plays a large role in survivorship for age-0 fish, both preceding and during winter. The faster and more efficiently a juvenile grows, the more likely it can evade or exceed the prey size preference of a given predator (Sogard, 1997; Kristiansen *et al.*, 2000). In addition to size-at-age when entering winter, food availability during the winter months also limits fish growth and (presumably) survival. Higher lipid stores increase the likelihood that fish will survive over winter (Henderson *et al.*, 1988). Condition indices, which researchers routinely use to indicate general fitness and energy storage, offer a means to evaluate these fat stores; they also offer a useful method to determine cod energy reserves (Bolger and Connolly, 1989; Grant and Brown, 1999). Cod store lipids in their liver and protein in their muscles, complicating measurement of condition in this species compared to fishes that store both lipid and protein in muscle tissue (Lambert and Dutil, 1997). Favourable condition prior to winter allows cod to metabolize large amounts of energy reserves and body tissues to cope with limited food availability (Black and Love, 1986), whereas fish in low condition may die of starvation overwinter (Dutil and Lambert, 2000). In freshwater systems, cold temperatures disproportionately impact smaller fish within a cohort because smaller fish begin winter with lower energy reserves and greater susceptibility to resource-limited environments (Post and Evans, 1989; Thompson *et al.*, 1991; Byström *et al.*, 2006). For this reason, post-winter condition of individual freshwater fishes depends primarily on their size prior to winter. However, there is poor understanding of this relationship in marine ecosystems.

The once abundant northern population of Atlantic cod declined dramatically in the 1980's and was ultimately placed under a fisheries moratorium in 1992 (Taggart *et al.*, 1994), which remains in place today (DFO, 2019). Noting its lack of recovery, research on early life stages of cod may provide important information on critical periods and survival bottlenecks. Atlantic cod in Newfoundland settle from pelagic to demersal habitat in several pulses through the summer and fall (Methven and Bajdik, 1994; Grant and Brown, 1998a; Ings *et al.*, 2008). A range in settlement times during this period results in multiple size-classes for age-0 Atlantic cod entering winter, creating a size-structured population from fall to spring. In size-structured populations, individual growth and mortality rates play a central role in determining population trajectories (Werner and Gilliam, 1984). More pronounced size-structured survival may characterize long, cold winters, with temperatures ranging from 2.1 to as low as -1.3 °C in coastal Newfoundland (Geissinger *et al.*, *submitted*). Although numerous studies demonstrate that temperature and food availability limit growth rates through winter for a variety of life stages (Krohn *et al.*, 1997; Grant and Brown, 1999; Otterlei *et al.*, 1999), no research has examined how variable size impacts the survival potential of age-0 cod entering their first winter, which potentially determines year class abundance.

Our study assesses the effect of size and food availability on growth, condition, and survival of age-0 demersal Atlantic cod in ambient coastal seawater conditions from January to April (-0.8 to 2.7 °C). We hypothesized that larger juvenile cod would survive longer and remain in better condition than smaller fish, but ration would have little impact on vital rates at such low regional temperatures. Collectively, these experiments allow us to assess the role of size and food availability in overwinter survival in age-0 cod in coastal Newfoundland.

5.3 Methods

5.3.1 Study sites and sampling method

We collected 530 age-0 Atlantic cod from Newman Sound, Terra Nova National Park, Newfoundland (48.58°N, -53.91°W) in November 2016, using a demersal seine net 25 m long, with 19 mm mesh, deployed 55 m from shore using a small boat and retrieved by two individuals standing 16 m apart on shore. The seine samples approximately 880 m^2 of habitat from the seabed to 2 m into the water column with a capture efficiency of 95% (Gotceitas *et al.*, 1997). Fish were then transported to the Ocean Sciences Centre in Logy Bay within 6 h for acclimation and experimental work.

5.3.2 Experimental design

We divided age-0 Atlantic cod into small (60-83 mm SL, standard length) and large (90-110 mm SL) size classes, and subdivided size classes across four feeding treatments (starvation, low food, medium food, high food). Based on relative body weight (BW), we anticipated <1% BW $\cdot$ d^{-1} food consumption in all feeding treatments (Gotceitas *et al.*, 1999), which is generally difficult to control in fish groups with potentially high competition for food (Karplus *et al.*, 2000). Therefore, we spread food for each feeding treatment across the tanks' surface daily, in a single pass, in order to minimize competition and ensure all fish had access to some food in the water column. Therefore, feeding rations (%BW $\cdot$ d^{-1}) were set higher than target levels (0.0% starvation; 2.5% low; 5%, medium; 10% high) based on dry mass conversion. This method increased the amount of uneaten food that remained on the bottom, which following removal and remeasurement (described below) yielded actual feeding treatments less than 1% BW · d^{-1} (Geissinger *et al.*, 2020). Atlantic cod were fed freeze dried krill (*Euphausia superba*) from JEHMCO Aquatic Breeder Supplies, Inc. (55% protein, 26% fat, 0.81% total carbohydrates, 461 kcal/100g). We configured 36 100-L rectangular tanks (65 x 42 x 38 cm), filled to a depth of 33.7 cm with ambient flow-through water system from a deep-water marine source at Ocean Sciences Centre of Memorial University, at an average flow rate of 33 $mL \cdot s^{-1}$. We randomly assigned treatment, fish size, and ration to tanks filled with seawater filtered through a 500 µm filter bag and maintained at ambient outside seawater temperature, which we measured twice daily (morning and evening). A total of 12 tanks with the large size class included three replicates of each feeding treatment level, and 24 tanks with the small size class included six replicates of each feeding treatment level (Fig. 5.1). Nine fish were assigned to each tank and acclimated and fed *ad libitum* for a 20-day acclimation period. Because we could not track individual fish throughout the study, each tank represented an individual measurement for growth and condition, with all measurements averaged within each tank. Ambient water temperature was 3.0 °C at the start of acclimation, declining to 2.2 °C by the initiation of our experiment. At Day 0, we euthanized 40 fish within each size class range from the holding tanks (18 small, 22 large) with tricaine methanesulfonate (TMS) to evaluate condition at the start of our experiment. We maintained tanks at ambient photoperiods, and water temperature was measured twice daily in each tank throughout our experiment. Salinity was stable at 32 ‰. The experiment began on 31 December 2016; we were compelled to terminate our experiment on 24 April 2017 under the terms of our animal care protocol.

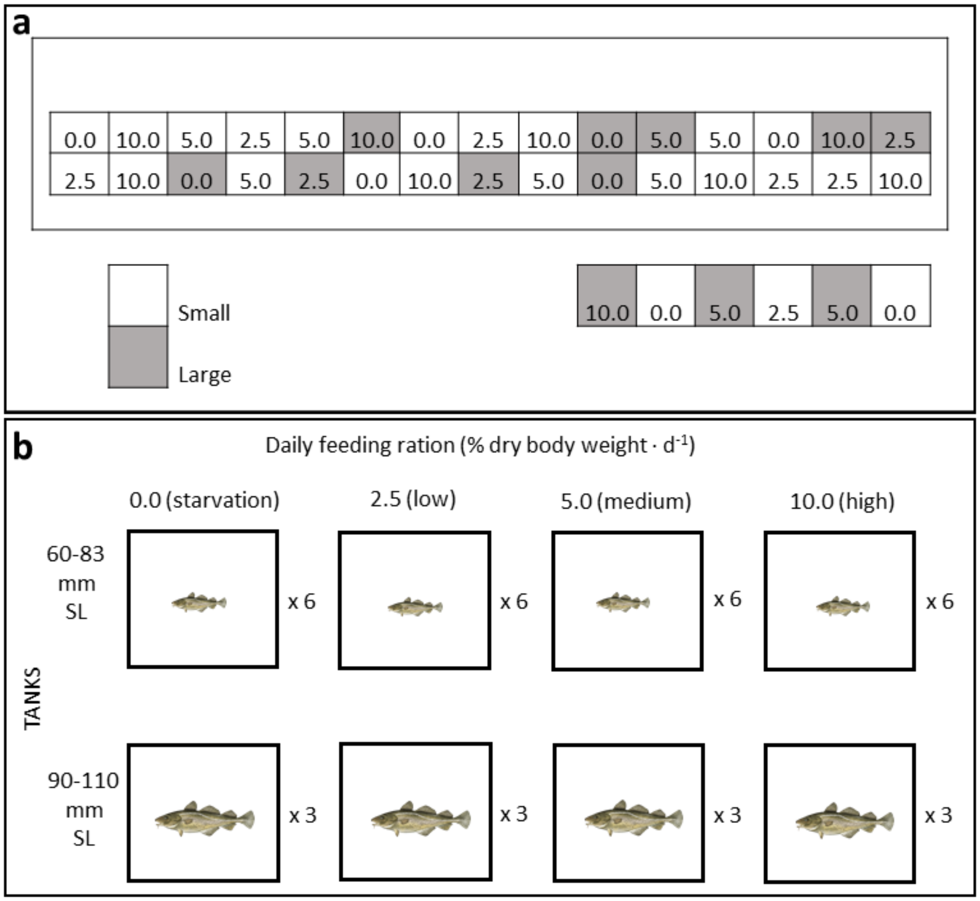

Figure 5.1. Conceptual diagram of experimental design. The top panel (a) represents the tank layout with size class and ration level (% dry body weight). The bottom panel (b) shows experimental design with treatment levels and sample size. Each square represents a tank, with 9 fish per tank at the start of the study. The size range represents the standard length (SL) of fish at the start of the study, with the small size class shown on top, and large size class shown on bottom.

We dried and weighed unconsumed food collected in each tank daily after the 90-min feeding period. Once a month, experimental animals were anaesthetized in 30 $mg \cdot L^{-1}$ TMS, then measured to determine length (±1 mm SL) and wet weight (±0.01 g; excess water was gently blotted away through a fine-meshed net), to adjust feeding ration and assess growth through the experiment.

Cod were checked twice daily, for survival and health. Using 100 $mg \cdot L^{-1}$ of TMS, we euthanized fish that lost equilibrium and did not react to mechanical prodding. We euthanized all surviving fish at the conclusion of our experiment on 24 April 2017. Length and weight were determined on these remaining fish as described above. After dissecting and weighing the liver of each fish, we also measured eviscerated wet weight, and stored liver and eviscerated bodies at -20 °C prior to drying the body and liver for 48 hours and 24 hours, respectively, at 65 °C (Lantry and O'Gorman, 2007); we determined dry weight on these individuals. All experiments undertaken during our investigation were conducted under MUN Animal Care Protocol #2016-02-RG.

5.3.3 Data analysis and statistical methods

Fulton's condition factor, K_{WET}, for wet weight was calculated as (Fulton, 1904):

$$K_{WET} = 100 \cdot (W_{WET} \cdot L^{-3}), \tag{1}$$

where W_{WET} was total wet weight (g) and L was standard length (cm). K_{WET} was calculated monthly for live fish. We calculated dry weight condition factor, K_{DRY}, at the end of the study, as (Grant and Brown, 1999):

$$K_{DRY} = 1000 \cdot (W_{DRY} \cdot L^{-3}), \tag{2}$$

where W_{DRY} was eviscerated dry weight. Loss of lipids and proteins can result in an increase of water content (Love, 1970; Grant and Brown, 1999); therefore, we considered dry weight more reliable than wet weight for condition measurements. We calculated hepatosomatic index (*HSI*) as (Lambert and Dutil, 1997):

$$HSI = 1000 \cdot (LW_{DRY} \cdot W_{DRY}^{-1}), \tag{3}$$

where LW_{DRY} was dry liver weight (g), and W_{DRY} was eviscerated dry weight.

We used juvenile fish sampled from the beginning of the experiment to calculate the change in K_{DRY} (ΔK_{DRY}) and *HSI* (ΔHSI) from Day 0 to termination by subtracting the final K_{DRY} and *HSI* from the mean initial K_{DRY} and initial *HSI* (Appendix 5.1; 5.2). We calculated specific growth rate for weight (SGR_W) according to the formula from Hawkins *et al*., (1985) as:

$$SGR_W = (\ln W_{WET2} - \ln W_{WET1}) \cdot (t_i - t_{i-30})^{-1} \cdot 100, \tag{4}$$

with W_{WET2} and W_{WET1} as total wet weights at times t_i and t_{i-30}. Fish were weighed and measured at 30-day intervals. We also calculated *SGR* for length (SGR_L) with length in place of weight.

We calculated a conversion factor for total remaining feed, accounting for water absorption. We ran trials with a known amount of food placed in each tank with no fish, dried, and then reweighed the residual food after the feeding period. The conversion factor was calculated as:

$$CF = W_f \cdot W_i^{-1}, \tag{5}$$

where *CF* denotes conversion factor, W_f is final weight of food after tank removal, and W_i refers to the initial weight of food before our treatments. This procedure yielded a conversion factor of 1.09. We therefore calculated daily total food consumption (g) as:

$$C = TF - (1.09 \cdot RF), \tag{6}$$

where TF was weight of total food (g) provided and RF was weight of remaining food (g). Feeding rate (F) was calculated as (Imsland *et al.*, 2006):

$$F = 100 \cdot \mathrm{C} \cdot [(W_{WET1}+W_{WET2})^{-1} \cdot 2] \cdot (t_i\text{-}t_{i\text{-}30})^{-1}, \tag{7}$$

where W_{WET1} and W_{WET2} were total wet fish weight (g) on days t_{i-30} and t_i at 30-day intervals. Feeding conversion efficiency (FCE) was calculated as (Imsland *et al.*, 2006):

$$FCE = (W_{WET2}\ \text{-}W_{WET1}) \cdot C^{-1} \tag{8}$$

We used the R statistical programming language (R Core Team, 2019) for all our statistical procedures and set $\alpha = 0.05$. We compared survival among treatments using the Kaplan-Meier estimator with the *survival* package (Therneau, 2015; Moore, 2016). We reported survival statistics include 95% confidence intervals. We used Pearson's product-moment correlation to determine the relationship between day of death and standard length for all mortalities. Correlation analyses were conducted on small, large, and combined size classes.

We analyzed live condition (K_{WET}) using a linear mixed effect model with the *lme4* package (Bates *et al.*, 2015). K_{WET} was the response variable, with ration (categorical), size (categorical), day of experiment (covariate), and tank (random effect) as the explanatory variables. We analyzed ΔK_{DRY} using a general linear model with Gaussian error distribution. We calculated mortality endpoint as the mean K_{WET} at time of death, using a general linear model with K_{WET} as the response variable and day of experiment as the explanatory variable. We analyzed final condition using ΔK_{DRY} as the response variable; explanatory variables included ration (categorical), size (categorical), and day of experiment (covariate). We treated tanks as replicates. We analyzed ΔHSI with the same model format. We report all condition values with standard error.

We analyzed SGR_W and SGR_L using a linear mixed effect model with the *lme4* package (Bates *et al.*, 2015) with ration (categorical), size (categorical), day of experiment (covariate), and tank (random effect) as explanatory variables. Feeding rate and feed conversion efficiency (*FCE*) were analyzed using a general linear model with Gaussian error distribution. The explanatory variables for both models were ration (categorical), size (categorical), and temperature (covariate). Statistical models excluded non-significant interactions ($\alpha > 0.05$). We have reported all growth values with standard error. Data calculations and visualizations were completed with *tidyverse* (Wickham, 2017). The associated data are available on Dataverse (Geissinger *et al.*, 2020). The associated statistical analysis outputs can be found in Appendix 5.3 – 5.9.

5.4 Results

5.4.1 Survival

Survival of large cod across all rations was greater than for small cod through the duration of the experiment, with large cod averaging 94.6% (CI[94.1,95.1], $n = 192$) survival at Day 80 in contrast to an average of 67.4% (CI[66.7, 68.1], $n = 266$) for small cod. Starvation resulted in the lowest survival for both large and small size classes, with consistently high survival in low (2.5% $BW \cdot d^{-1}$), medium (5.0% $BW \cdot d^{-1}$), and high (10.0% $BW \cdot d^{-1}$) rations (Fig. 5.2). Reduced survival (58.2%, CI[56.7, 59.7], $n = 38$) in small cod under starvation at Day 60 contrasted high survival (93.9%, CI[92.9, 95.0], $n = 50$) in large cod under starvation. Small cod in the starvation treatment declined steadily throughout the study, in contrast to high survival in large cod until Day 64. Day of death did not correlate with standard length for the small size class ($r = 0.16$, $p = 0.18$, $df = 69$), or the large size class ($r = 0.044$, $p = 0.87$, $df = 13$). For the study population as a whole, a significant correlation ($r = 0.52$, $p < 0.001$, $df = 84$) between day of death during the experiment and length suggested size-dependent survival between the large and small size classes, with the small size class largely driving the relationship.

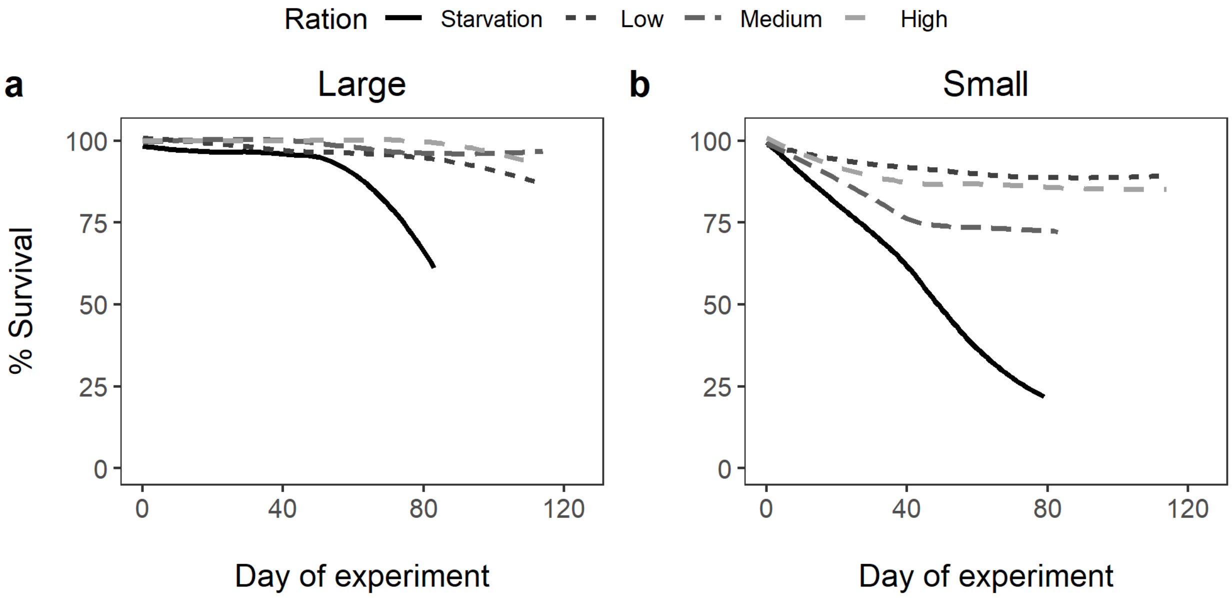

Figure 5.2. Percent survival of (a) large, 90-110 mm SL and (b) small, 60-83 mm SL, juvenile Atlantic cod (*Gadus morhua*) under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]) (n=24 small size class, 12 large size class tanks), with 9 fish per tank.

5.4.2 Condition

Condition (K_{WET}) decreased significantly through the duration of our starvation trials for small and large cod relative to the other rations (ANODEV, $\chi^2 = 167.89$, $p < 0.05$, df = 3,26); size had an interactive effect with duration of study (ANODEV, $\chi^2 = 13.70$, $p < 0.05$, df = 1,26). K_{WET} in the small size class decreased from 0.83 ± 0.02 on Day 0 to 0.67 ± 0.01 on Day 80 (Fig. 5.3a), and in the large size class decreased from 0.86 ± 0.01 to 0.62 ± 0.01 on Day 84 (Fig. 5.3b). K_{WET} changed over time in our starvation trials, $K_{WET} = 0.839 - 0.002t$, where t was day and 0.839 was the starting condition. For the low, medium, and high rations, in both the small and large size classes, K_{WET} remained effectively constant (Fig. 5.3). Small juvenile cod reached a mortality endpoint at $K_{WET} = 0.608$ (± 0.021); large juvenile cod reached this endpoint at $K_{WET} = 0.589$ (± 0.016). Small juvenile cod reached a lethal condition after 115.5 days, and large juvenile cod reached lethal condition after 125 days.

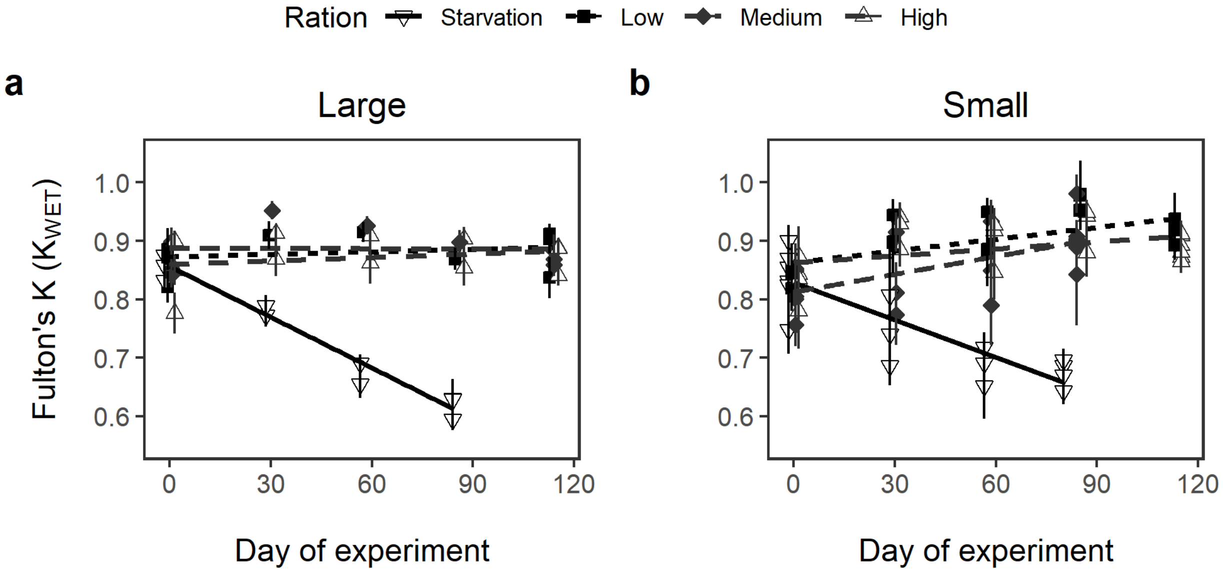

Figure 5.3. Fulton's condition factor K (K_{WET}) of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]), during 30-day intervals (n=24 small size class, 12 large size class tanks). Vertical error bars represent ± se. K_{WET} between size groups did not differ significantly (ANODEV, $\chi^2 = 3.71$, $p = 0.054$). K_{WET} under starvation differed significantly among low, medium, and high rations (ANODEV, $\chi^2 = 3206.03$, $p < 0.05$).

Change in dry weight condition (ΔK_{DRY}) was larger in fish fed the low, medium, and high rations than the starvation treatment (ANOVA, $F = 9.56$, $p < 0.05$, df = 3,31; Fig. 5.4), and size class also affected ΔK_{DRY}, with a larger difference in condition for small fish than large fish

(ANOVA, F = 5.94, p = 0.02, df = 1,31; Fig. 5.4). The ΔK_{DRY} = -0.27 ± 0.04 in small cod under starvation contrasted ΔK_{DRY} of -0.43 ± 0.03 in larger cod. Increasing ration beyond the lowest level (2.5%) had no further positive impact on condition. The ΔK_{DRY} = 0.02 ± 0.02 for low and medium rations was similar to ΔK_{DRY} = 0.03 ± 0.05 for the high ration (Fig. 5.4).

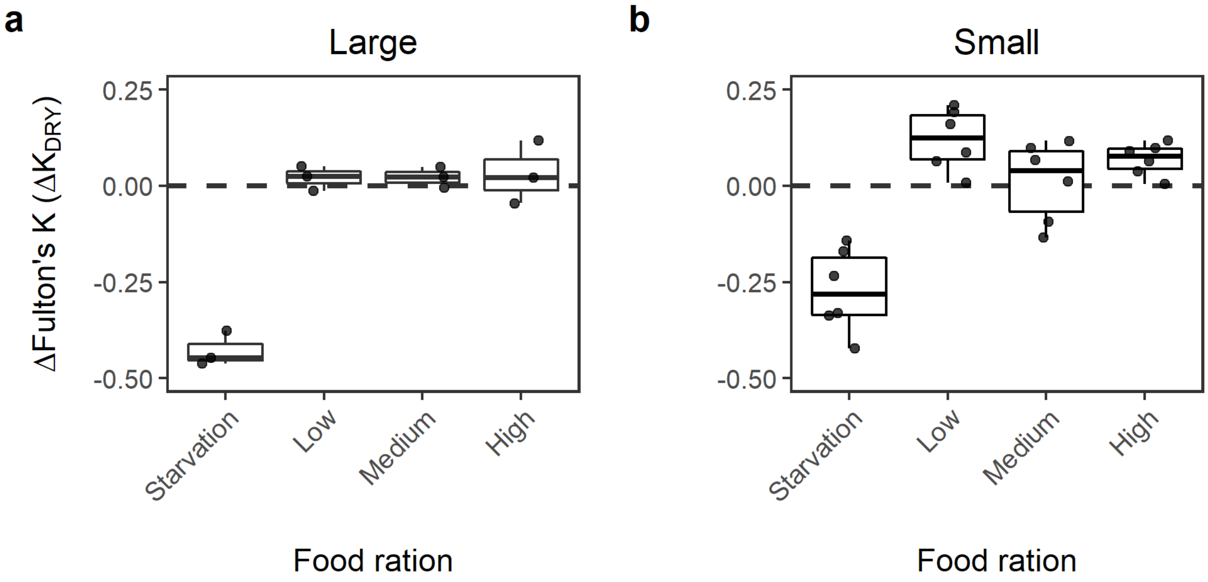

Figure 5.4. Change in Fulton's condition factor K (ΔK_{DRY}) of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]) (n=24 small size class, 12 large size class tanks). The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Individual points represent ΔK_{DRY} values by tank. ΔK_{DRY} in starvation treatment differed significantly among low, medium, and high rations (ANOVA, F = 49.56, p <0.05), and size significantly affected ΔK_{DRY} (ANOVA, F = 5.94, p = 0.02).

Size class strongly affected *ΔHSI* (ANOVA, F = 37.42, p < 0.05, df = 1,23). The *ΔHSI* in large cod decreased by 0.53 from small cod. Ration did not significantly affect *ΔHSI* (ANOVA, F = 0.02, p = 0.99, df = 3,23) varying less than 0.03 in all rations, relative to the starvation treatment. Although the effect was not statistically significant, the data trend suggested that positive *ΔHSI* in small cod increased with increase in ration (Fig. 5.5a), whereas *ΔHSI* in large cod decreased with increase in ration (Fig. 5.5b).

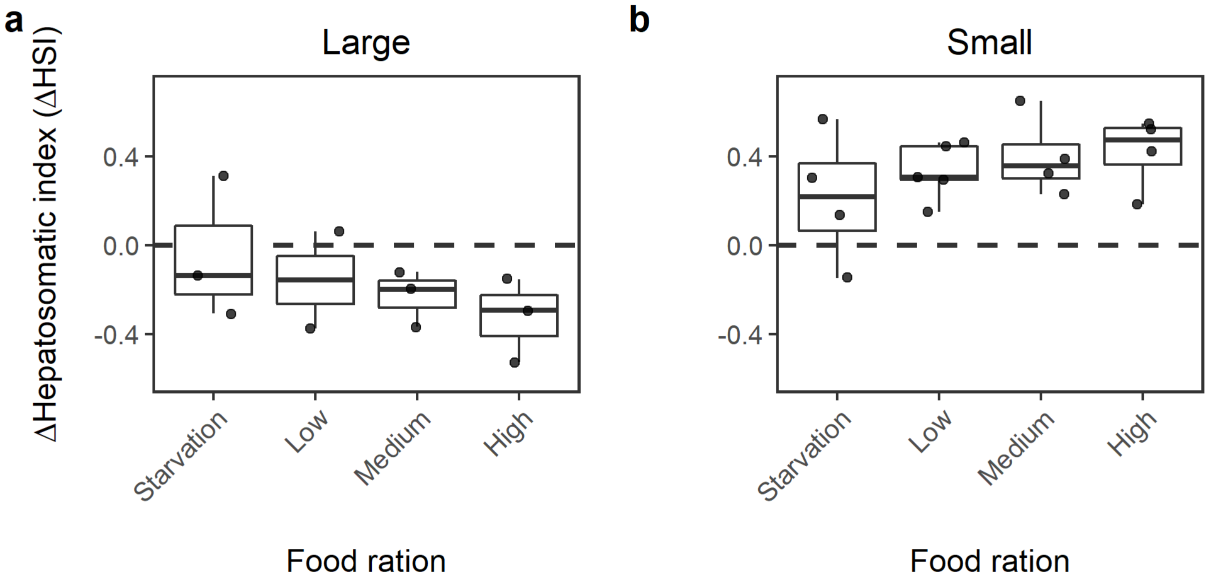

Figure 5.5. Mean change in hepatosomatic index (*ΔHSI*) by tank of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]) (n=24 small size class, 12 large size class tanks). The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Individual points represent *ΔHSI* values by tank. Size (ANOVA, F = 37.42, p <0.05) significantly influenced *ΔHSI*.

5.4.3 Growth

Size class had no effect on SGR_W (ANODEV, $\chi^2 = 0.27$, $p = 0.606$, df = 1,51) or on SGR_L (ANODEV, $\chi^2 = 3.37$, $p = 0.066$, df = 1,51). We observed decreased weight in the starvation treatment with an SGR_W of -0.249 ± 0.059 % g · d^{-1} (Fig. 5.6a). SGR_L increased slightly for length (0.039 ± 0.013 % mm · d^{-1}), but this increase likely reflects size-selective mortality in tanks (Table 5.1; Fig. 5.6b). Weight increased in all other rations (ANODEV, $\chi^2 = 277.89$, $p < 0.05$, df = 3,51), as did length (ANODEV, $\chi^2 = 42.78$, $p < 0.05$, df = 3,51), but did not differ significantly among treatments. SGR_W was identical for the low ration (0.45 ± 0.02 %g · d^{-1}), and the medium ration (0.45 ± 0.04 %g · d^{-1}), in contrast to the high ration (0.38 ± 0.01 %g · d^{-1}; Fig. 5.6a). SGR_L was also identical for the low ration (0.11 ± 0.01 %mm · d^{-1}) and medium ration (0.11 ± 0.02 %mm · d^{-1}), similar to the high ration (0.10 ± 0.01 %mm · d^{-1}; Fig. 5.6b).

Table 5.1. Size-selective mortality of cod in starvation treatment. Standard length (SL) of mortalities was measured throughout the 30-day time interval. SL of live cod was measured on the last day of each time interval.

Time interval (days)	Size Class	Mean mm SL cod mortalities ± se (n)	Mean mm SL live cod ± se (n)
0-31	Small	70.60 ± 1.22 (16)	78.03 ± 0.89 (38)
32-59	Small	76.20 ± 1.30 (18)	79.43 ± 1.16 (20)
60-80	Small	78.90 ± 1.39 (7)	80.15 ± 0.87 (13)
0-31	Large	108.00 (1)	104.54 ± 0.63 (26)
32-59	Large	99.00 (1)	105.50 ± 0.68 (25)
60-84	Large	103.00 ± 0.43 (7)	106.06 ± 0.87 (18)

*Live cod were measured on the last day of each time interval

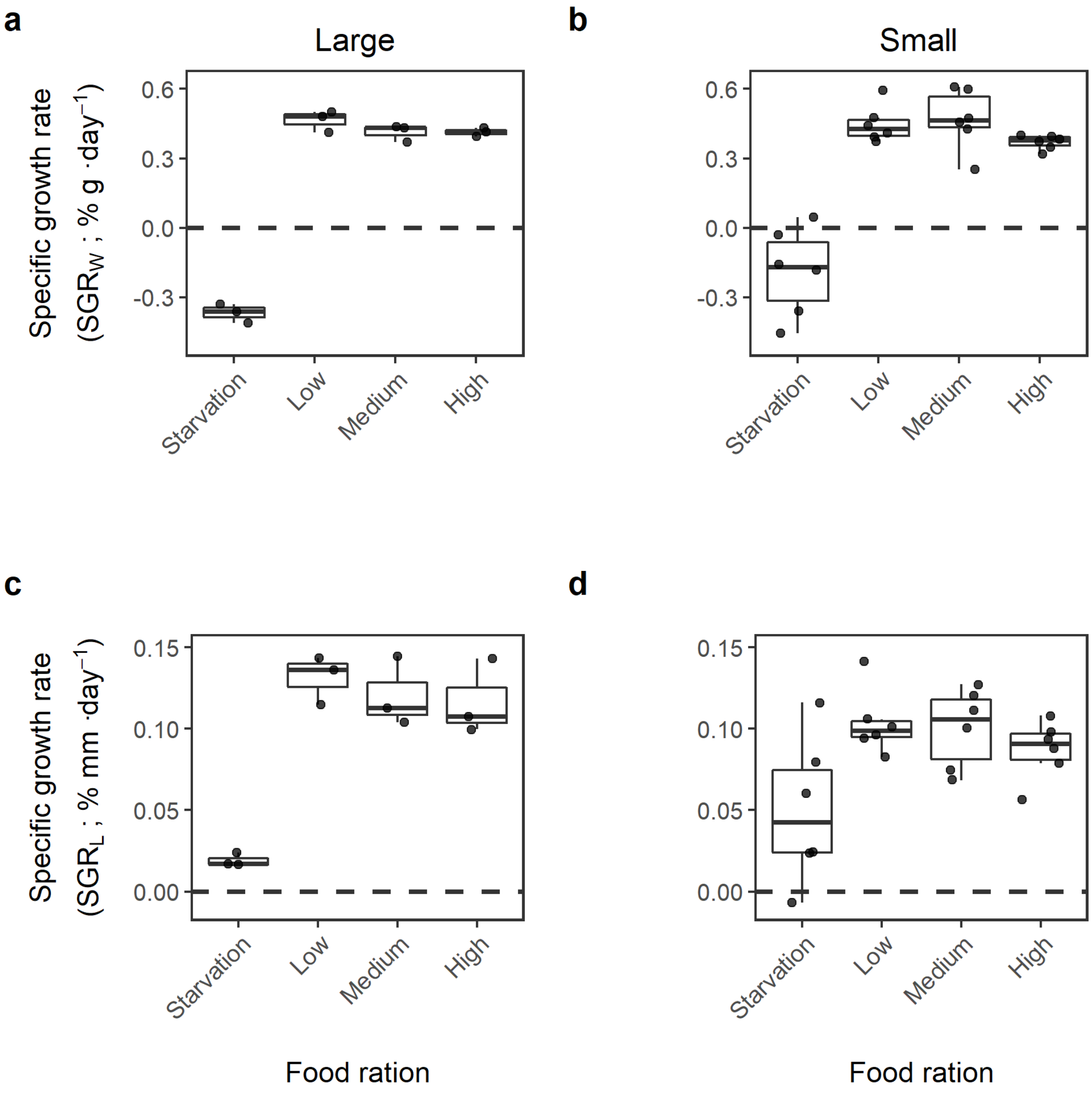

Figure 5.6. Specific growth rate of weight (SGR_W) for (a) large and (b) small juvenile Atlantic cod, and specific growth rate of length (SGR_L) for (c) large and (d) small juvenile Atlantic cod under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]) (n=24 small size class, 12 large size class tanks). The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Individual points represent *SGR* values by tank. Size did not significantly affect SGR_{W} (a, b; ANODEV, $\chi^2 = 0.27$, p = 0.61), or SGR_L (c, d; ANODEV, $\chi^2 = 3.37$, p = 0.07). The starvation treatment differed statistically among low, medium, and high rations for SGR_W (a, b; ANODEV, $\chi^2 = 277.89$, p <0.05) and $\mathrm{SGR_L}$ (c, d; ANODEV, $\chi^2 = 42.78$, p <0.05).

5.4.4 Feeding and conversion efficiency

Feeding rate ranged from 0.19 - 0.45 % BW·d^{-1} in the low ration, 0.24 - 0.55 % BW·d^{-1} in the medium ration, and 0.28 – 0.61 % BW·d^{-1} in the high ration. Size did not influence feeding rate (ANOVA, F = 0.91, p = 0.34, df = 1,97) but feeding rate increased with increasing feeding ration (ANOVA, F = 11.51, $p < 0.05$, df = 2,97). The feeding rate of fish in the high ration treatment was approximately 0.04 % BW·d^{-1} higher than fish observed in the medium and low ration treatments. Fish in the medium and low ration treatments did not differ significantly in their feeding rate (Fig. 5.7). Feeding rate decreased significantly at lower ambient temperatures (ANOVA, F = 279.20, $p < 0.05$, df = 1,97; Fig. 5.7). Temperature ranged from -0.7 °C to 2.5 °C (Fig. 5.8), with the lowest temperature on Day 95 (4 April 2017) when pack ice moved into the bay, as is typical in the spring.

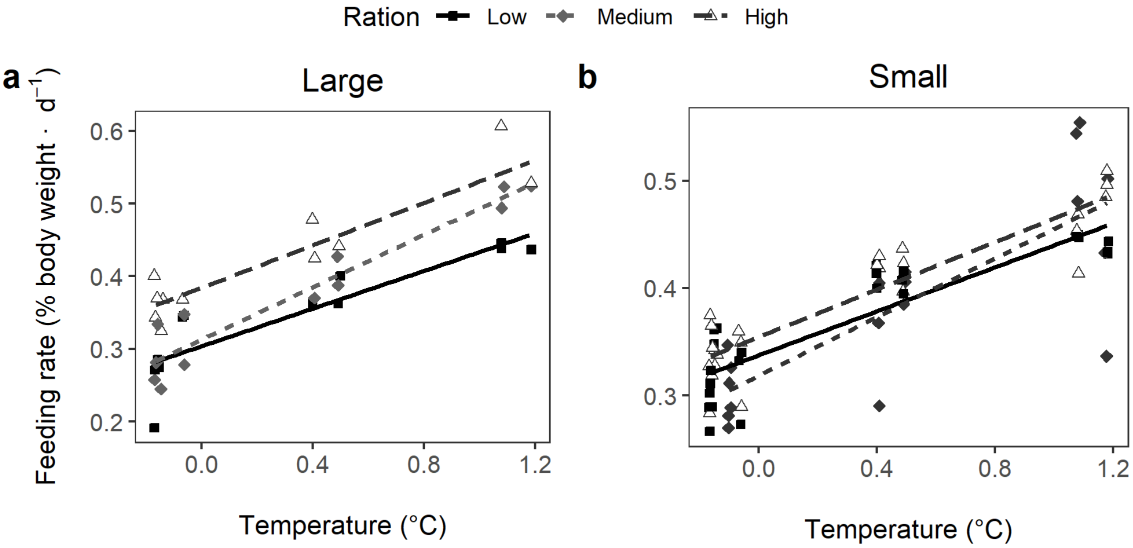

Figure 5.7. Feeding rate of (a) large (b) small juvenile Atlantic cod and mean temperature during 30-day intervals under low (2.5%), medium (5.0%), and high (10% dry body weight) rations. We calculated food consumption by tank (n=24 small size class, 12 large size class tanks) averaging across 30-day intervals. Feeding ration significantly affected feeding rate (ANOVA, F = 11.51, p <0.05), but size did not (ANOVA, F = 0.91, p = 0.34). Temperature strongly affected feeding rate (ANOVA, F = 279.20, p <0.05).

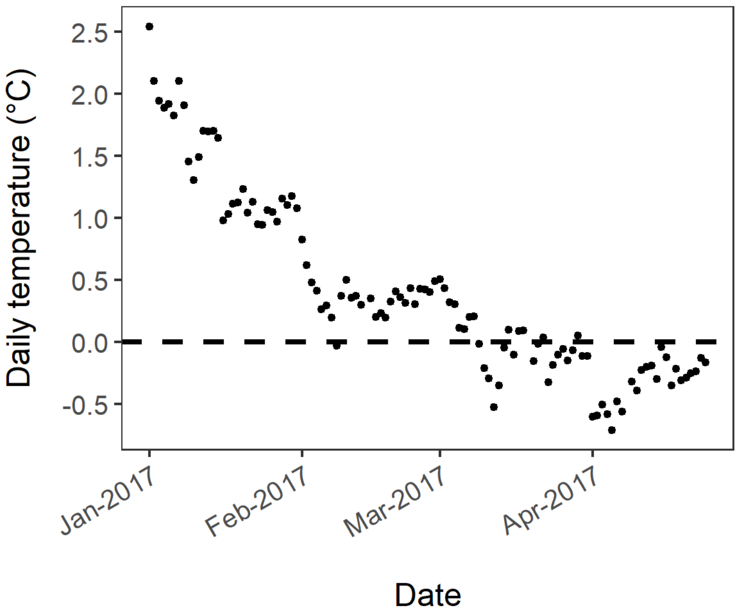

Figure 5.8. Mean daily temperatures of experimental tanks (n=36) from 31 December 2016 to 24 April 2017. Tanks were 100-L with ambient flow-through water system from a deep-water source at Ocean Sciences Centre of Memorial University of Newfoundland, at an average flow rate of 33 mL·s^{-1}.

Across all rations, significantly higher *FCE* characterized large cod compared to small cod (ANOVA, F = 7.15, $p < 0.05$, df = 1,109), with the small size *FCE* decreasing by 0.29 (±011) relative to the large size fish. *FCE* changed with ration (ANOVA, F = 4.48, p = 0.01, df = 2,109; Fig. 5.9). The medium ration had a 0.37 (±0.13) decrease in *FCE* relative to the low ration, and the large ration had a 0.27 (±0.12) decrease in *FCE* relative to the low ration. Ambient temperature had no significant effect on feed conversion efficiency (*FCE*; ANOVA, F = 3.44, p = 0.066, df = 1,109).

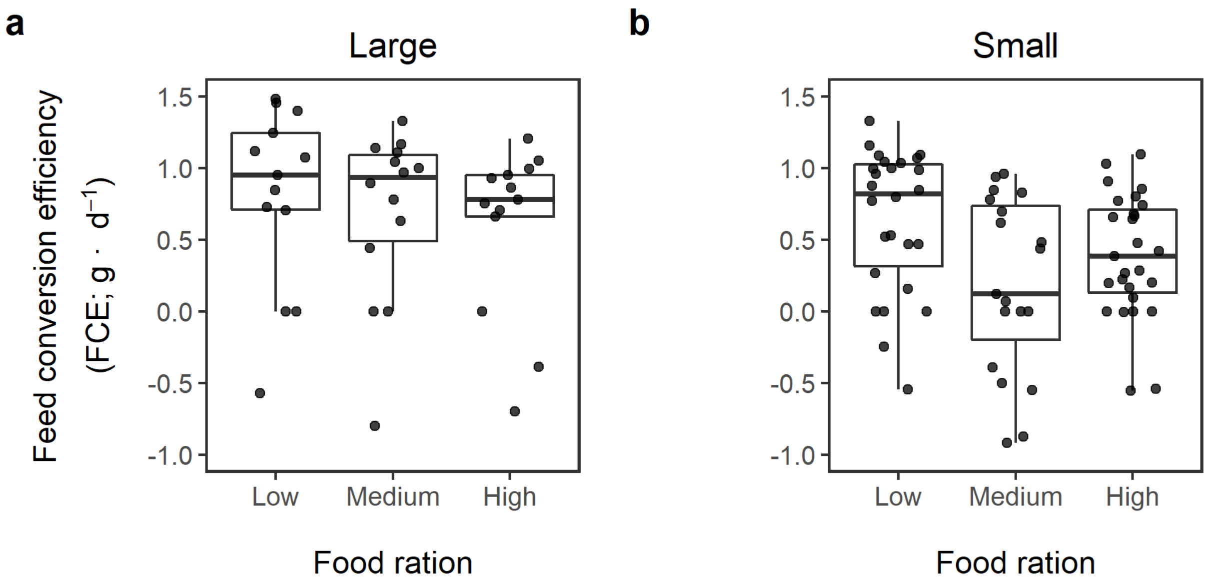

Figure 5.9. Feed conversion efficiency (*FCE*) of (a) large and (b) small juvenile Atlantic cod for low (2.5%), medium (5.0%), and high (10.0% dry body weight) rations. The bold line represents the median. The lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x of the interquartile range. Individual points represent the value for each tank (n=36; 24 small size class, 12 large size class tanks) averaged across 30-day intervals. Size (ANOVA, F = 7.15, $p < 0.05$) and ration (ANOVA, F = 4.48, $p < 0.05$) both significantly affected *FCE*.

5.5 Discussion

Our results did not support our initial hypothesis that changes in food availability would significantly impact growth, condition, or survival of age-0 Atlantic cod overwintering in coastal Newfoundland. Rather, modest rations (0.2 – 0.6% dry body mass · d^{-1}) positively affected condition, growth, and survival compared to starvation levels, but additional food levels produced no further significant improvement in these metrics. Improved survival, condition, growth, and feeding rate all point to the importance of food presence for overwinter growth and survival, especially in small juveniles. Overwinter starvation results in low energy reserves and potential death in winter durations typical of north temperate and subarctic marine conditions.

Food availability in winter varies across regions. Zooplankton biomass decreases as winter temperatures decrease in Prince William Sound, Alaska (Foy and Paul, 1999), whereas abundant food availability in areas of northern Norway overwinter maintains or improves condition in sea trout (*Salmo trutta*; Rikardsen *et al.*, 2006). Despite limited understanding of overwinter food availability in coastal Newfoundland, limited food availability could potentially occur during winter. We have sometimes observed low condition (Fulton's $K<0.60$; Geissinger *et al.*, *submitted*) in wild age-1 Atlantic cod collected post-winter, similar to fish sampled from starvation treatments in this study. Grant and Brown (1998b) observed a shift in diet from autumn to early winter, with age-0 cod diet dominated by small crustacea zooplankton in the autumn, shifting to small copepods (e.g., *Pseudocalanus* sp., *Acartia* sp.) in November and December, and both ration size and size of zooplankton declined through December, possibly associated with decreased temperature (Grant and Brown, 1998b). Nonetheless, diet, prey availability, and food consumption for age-0 cod after December is poorly understood as temperatures decrease and fish move into deeper water (Methven and Bajdik, 1994).

Previous studies in freshwater emphasize the importance of size for overwinter survival (Post and Evans, 1989; Huss *et al.*, 2008), which our study confirms for a marine environment. Small fish in our study starved to death faster than large fish. Although both size groups reached a critical point (necessitating ethical termination of our trials), we observed much lower mortality of large cod in the starvation treatment ($0.55\% \cdot d^{-1}$) than in small cod ($2.21\% \cdot d^{-1}$). Our results show that juvenile cod risk starving to death over winter, and larger cod entering winter have a greater chance of surviving longer than smaller cod. Low energy reserves can also increase susceptibility to predator attack and capture because of energy depletion (Jonas and Wahl, 1998). Although large juveniles in our study also depleted their energy reserves, they reached a critical point later than small cod (Day 78 compared to Day 54), showing that larger fish have a survival advantage during longer winters. The condition endpoints and loss of Fulton's K over time provide an overwinter mortality predictor for juvenile Atlantic cod, which could be a useful tool for fisheries management. For example, assuming no access to food during winter, survival probabilities of individual fish sampled prior to or during winter could be estimated based on size, starting condition, and estimated duration of winter.

High mortality of small juveniles in our study relates to depletion of energy reserves (Huss *et al.*, 2008). Cold-water marine juvenile fish often accumulate lipids during late summer and autumn to store excess energy for the overwinter period (Copeman *et al.*, 2017). These fat reserves play a critical role in low-food situations. Age-0 sand smelt (*Athlerina boyeri*) accumulate fat reserves from September to November, with larger smelt building up more fat reserves than small individuals (Henderson *et al.*, 1988). Previous work in Newfoundland, however, showed that juvenile Atlantic cod do not increase condition or relative amounts of lipids during late summer and early fall, but size nonetheless influences lipid amounts in age-0 cod, with higher total lipids in smaller juveniles compared to larger juveniles (Copeman *et al.*, 2008). The higher total lipids in small juveniles, therefore, could potentially help them endure winter. However, for small juveniles to maintain condition throughout winter, food must be present in the system. Our results differ from freshwater systems where large and small lake herring declined in condition in fed and starved feeding treatments, with the largest decline in starved treatments (Pangle *et al.*, 2004). In contrast, our results showed that juvenile Atlantic cod maintain condition with varying levels of food, so that rations above 2.5% dry body mass · d^{-1} did not improve condition or growth.

However, at starvation levels, condition decreased significantly for both small and large groups. Although survival time differed between small and large size classes at the starvation level, condition did not differ between the two size classes. Our results are in line with an overwinter study on age-0 Arctic char (*Salvelinus alpinus*) that reported differences in survival time between size classes, with larger char surviving longer than small char, but with no difference in lipid mass between the two size groups (Byström *et al.*, 2006). Age-0 fish are known to use stored energy reserves through the winter (Post and Evans, 1989; Hurst and Conover, 2003; Finstad *et al.*, 2004) and, as shown in our study, where highest mortality and poorest condition factor occurred in our starvation treatment, risk significant energy loss throughout winter.

Small juveniles experienced depleted condition and high mortality in the absence of food, indicating these fish are highly reliant on ample pre-winter stored energy. However, in the presence of food, it is unclear if juveniles use stored energy, because both large and small juvenile cod maintained their condition, regardless of how much food was available. Unexpectedly, more food did not translate into increased condition or growth. Potential causes could be either limited uptake or energetic cost to digest the additional food, therefore negating energy gain. Food consumption ranged from 0.2 – 0.6% dry body mass · d^{-1}, which was less than our supplied ration. However, cod consumed higher amounts of food when provided larger rations, indicating that limited uptake may not have maintained condition and growth. Alternatively, cod may have higher energetic costs associated with digesting food, as seen with decreased feed conversion efficiency (*FCE*) with increased ration.

The trend in the hepatosomatic index (ΔHSI) differed from that in Fulton's K (ΔK_{DRY}). Small cod maintained HSI under starvation conditions and increased HSI with increased food ration. However, large juveniles depleted HSI as food availability increased. These two trends may represent two alternative strategies for age-0 fishes: energy storage and somatic growth. Potentially, limited capacity to draw on lipid stores in small juvenile livers for the duration of winter may contrast with large juveniles that continue to draw from liver lipid stores over the course of winter (Hemre *et al.*, 1993). Despite higher HSI in large compared to small age-0 cod at the start of our study, cod in our overwinter experiment showed a strategy opposite that reported for freshwater ecosystems (Post and Parkinson, 2001), with large cod investing in somatic growth, whereas small cod invested in energy storage. Therefore, large juveniles may use liver energy stores while investing in growth and body condition, whereas small juveniles invest energy into liver stores as resources become available.

Cod increased in both weight and length with the presence of food but invested more energy to increasing weight rather than length under feeding conditions. This pattern is consistent with an energy allocation strategy opposed to somatic growth (Mogensen and Post, 2012). A previous study on growth and survival in age-0 Atlantic cod (Gotceitas *et al.*, 1999) reported no difference in SGR at two feeding rations, 0.25% and 1.0% body weight·d^{-1} with temperatures ranging from -0.95 (± 0.06) to 2.46 (±0.37) °C. In freshwater systems, age-0 largemouth bass (*Micropterus salmoides*) increased in weight when fed in warm winters but decreased in cold winters with a temperature low of ~1 °C (Fullerton *et al.*, 2000). In contrast, juvenile cod in our study gained weight at low temperatures (-0.7 to 2.5 °C) when fed. Juvenile cod in coastal Newfoundland appear to allocate energy towards storage in the winter, in sharp contrast to allocation to size (length) in the summer and fall period (Copeman *et al.*, 2008). This switch likely represents shifting relative risk from size-dependent predation in smaller cod in summer (Sogard, 1997; Linehan *et al.*, 2001; Copeman *et al.*, 2008), to increased starvation risk in winter.

The size-dependent survival, growth, and condition observed in our study link mechanistically to ontogenetic changes in metabolism, behavior, and conversion efficiencies observed in Atlantic silverside (*Menidia menidia*; Schultz and Conover, 1999), Atlantic cod (Imsland *et al.*, 2006), and rainbow trout (*Oncorhynchus mykiss*; Mogensen and Post, 2012). Other fish species, such as muskellunge (*Esox masquinongy*) show size-dependent trends related to winter temperatures (Chipps *et al.,* 2000), but with large variation among species, including bluegill (*Lepomis macrochirus*; Wohlschlag and Juliano, 1959), lake charr (*Salvelinus namaycush*), and walleye (*Stizostedion vitreum vitreum*; William and Beamish, 1990). In our study, juvenile cod feeding rate declined at temperatures below 0 °C. Low metabolic rates associated with temperature reduce food requirements and, by also reducing energetic activity (e.g., age-0 smelt, *Atherina boyeri*), fish may completely cease feeding during the winter (Henderson *et al.*, 1988). In marine temperate systems, juvenile Atlantic cod and haddock (*Melanogrammus aeglefinus*) reduced food consumption by 80% when temperature decreased from 11 °C to 2 °C (Pérez-Casanova *et al.*, 2009), and food consumption for juvenile Atlantic cod declined as temperature decreased from 8.3 °C to 0.6 °C (Brown *et al.*, 1989). Higher food conversion efficiency in large cod compared to small cod, in our study, could result from size-dependent differences in metabolic, biochemical, or behavioral activity (Kerr, 1971). However, the negative relationship between food ration and conversion efficiency (as observed within the small fish of this study) typifies patterns observed in other fish species (e.g., tilapia, *Oreochromis niloticus*, Meyer-Burgdorff *et al.*, 1989; turbot, *Scophthalmus maximus*, Van Ham *et al.*, 2003; rainbow trout, Wurtsbaugh and Davis, 1977) that previous studies generally attributed to increased energy expenditure for digestion – i.e., specific dynamic action (SDA, Jobling, 1981) – or increased activity (Wurtsbaugh and Davis, 1977). Because fish in our study showed no signs of increased activity, increased SDA from high feeding rates offers a likely mechanism to explain the decline in food conversion efficiency.

When even low-levels of food are available (<1% BW·d^{-1}), age-0 juvenile cod in Newfoundland should be able to continue to grow and maintain condition through the spring, irrespective of their size at the start of winter. Based on our experimental results, and observations of prey items in the stomachs of juvenile cod in the early winter (Grant and Brown, 1998b), we expect relatively low size-selective survival compared to other systems (Tsukamoto *et al.*, 1989; Garvey *et al.*, 1998; Byström *et al.*, 2006), but that increased size-selective mortality in juvenile cod could become more important as winters become warmer and metabolically more stressful in scenarios with no food availability. Although largely nutrient poor, many Newfoundland fjords experience pulses of high productivity when on-shore wind events transport nutrient-rich water into the fjord (Syvitski *et al.*, 1987; Ings *et al.*, 2008). Therefore, characterizing both the timing and magnitude of food availability in overwintering habitats offer important future research directions regarding overwinter dynamics in juvenile Atlantic cod.

5.6 Acknowledgements

This research was sponsored by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada (including Productive Capacity and Marine Conservation Targets programs) and INREST (representing the Port of Sept-Îles and City of Sept-Îles, Quebec). We thank Christine Vickers, the workshop staff at Ocean Sciences Centre, and Phil Sargent for their help in the laboratory and field. An additional thanks to Emma Cooke, Evelyn MacRobert, and Salma Husaien for assisting with data collection. The manuscript benefitted from the numerous suggestions of Louise Copeman and Chris Parrish. Our lab research was conducted under Memorial University of Newfoundland, Animal Care Protocol #2016-02-RG.

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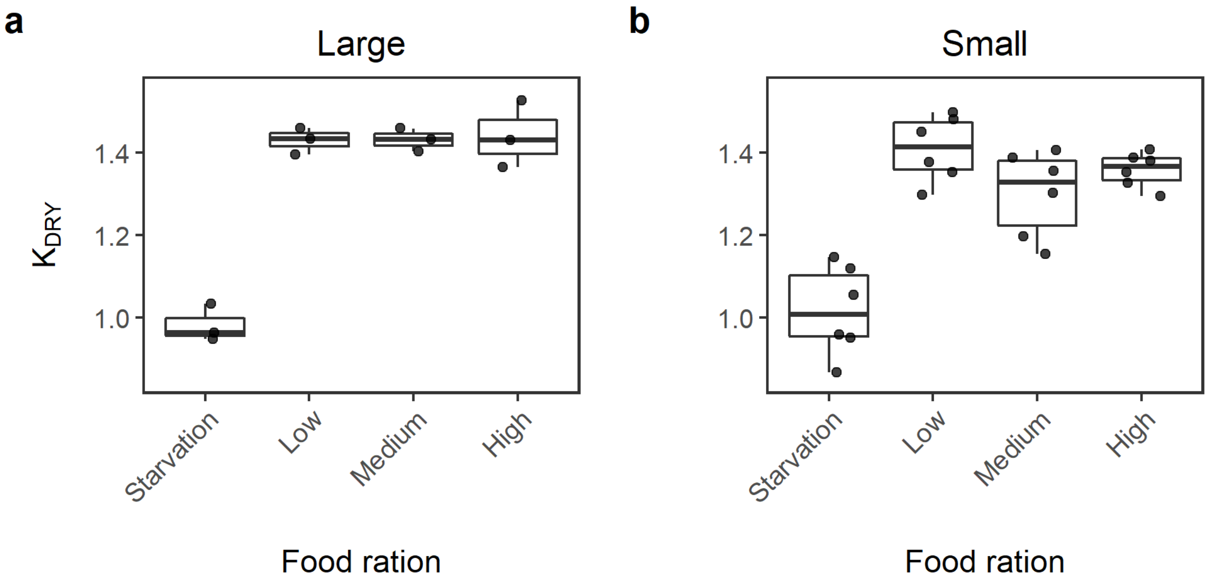
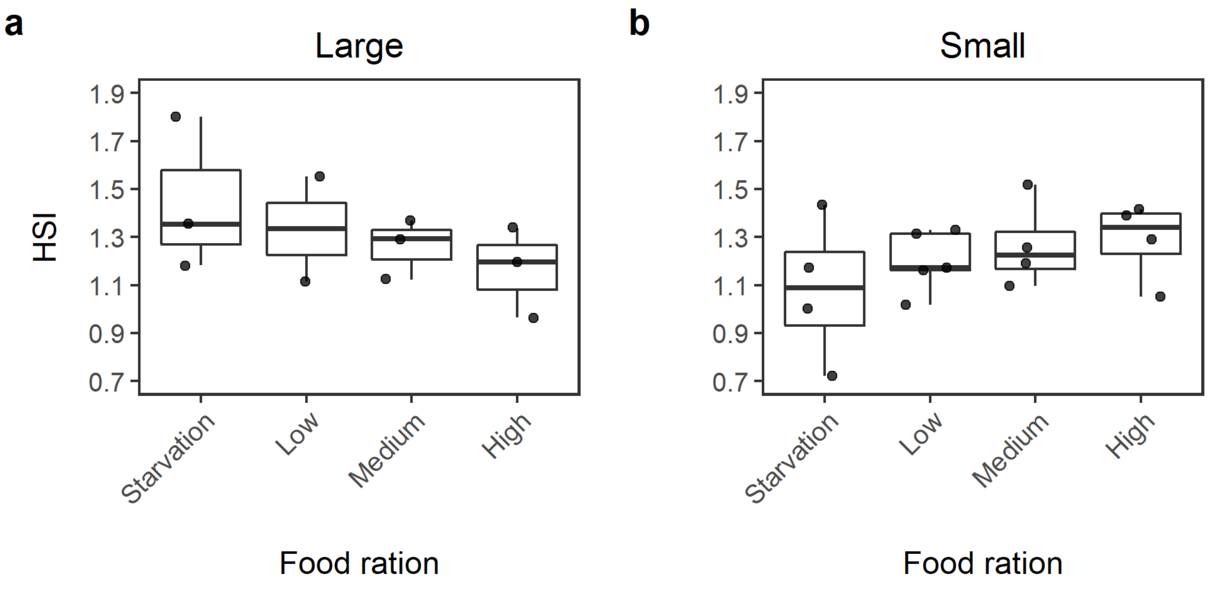
5.8 Appendix



Appendix 5.1. Fulton's condition factor K (K_{DRY}) of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]) (n=24 small size class, 12 large size class tanks). The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Individual points represent K_{DRY} values by tank.



Appendix 5.2. Mean hepatosomatic index (*HSI*) by tank of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation [0.0%], low [2.5%], medium [5.0%] and high [10% dry body weight]) (n=24 small size class, 12 large size class tanks). The bold line represents the median. The lower and upper hinges correspond to the first and third quantiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5x the interquartile range. Individual points represent *HSI* values by tank.

Appendix 5.3. Analysis of Deviance table for the effect of size and ration on Fulton's condition factor K (K_{WET}) over the duration of the experiment. Model was written as a general linear model with repeated measures (tank). Error distribution is Gaussian with an identity link (n=116).

Explanatory Variable	**Chi-square**	**DF**	**P-value**
Intercept	3206.03	1	<0.001
Ration	3.77	3	0.287
Size	3.71	1	0.054
Day of Experiment	150.35	1	<0.0001
Ration x Day of Experiment	167.89	3	<0.0001
Size x Day of Experiment	13.70	1	.0002

Appendix 5.4. Analysis of Variance table for the effect of size and ration on change in Fulton's condition factor K (ΔK_{DRY}). Model was written as a general linear model with Gaussian error distribution (n=36).

Explanatory Variable	Sum of Squares	DF	F-Value	P-value
Intercept	0.83	1	125.13	<0.0001
Ration	0.99	3	49.56	<0.0001
Size	0.04	1	5.94	0.02
Residuals	0.21	31		

Appendix 5.5. Analysis of Variance table for the effect of size and ration on change in hepatosomatic index (ΔHSI). Model was written as a general linear model with Gaussian error distribution (n=36).

Explanatory Variable	Sum of Squares	DF	F-Value	P-value
Intercept	0.64	1	12.98	0.0015
Ration	0.0035	3	0.024	0.99
Size	1.85	1	37.42	<0.0001
Residuals	1.14	23		

Appendix 5.6. Analysis of Deviance table for the effect of size and ration on specific growth rate (SGR_W). Model was written as a general linear mixed effect model with Gaussian error distribution and identity link (n=36).

Explanatory Variable	Chi-square	DF	P-value
Ration	277.89	3	<0.0001
Size	0.27	1	0.606
Day of Experiment	14.29	1	0.0002

Appendix 5.7. Analysis of Deviance table for the effect of size and ration on specific growth rate (*SGR_L*). Model was written as a general linear mixed effect model with Gaussian error distribution and identity link (n=36).

Explanatory Variable	**Chisquare**	**DF**	**P-value**
Ration	42.78	3	<0.0001
Size	3.37	1	0.066
Day of Experiment	4.15	1	0.041

Appendix 5.8. Analysis of Variance table for the effect of size, ration, and temperature on feeding rate. Model was written as a general linear model with Gaussian error distribution and identity link (n=143).

Explanatory Variable	**Sum of Squares**	**DF**	**F-Value**	**P-value**
Intercept	2.13	1	1323.24	<0.0001
Ration	0.037	2	11.51	<0.0001
Size	0.0015	1	0.91	0.34
Temperature	0.45	1	279.20	<0.0001
Residuals	0.16	97		

Appendix 5.9. Analysis of Variance table for the effect of size, ration, and temperature on food conversion efficiency (*FCE*). Model was written as a general linear model with Gaussian error distribution and identity link (n=114).

Explanatory Variable	**Sum of Squares**	**DF**	**F-Value**	**P-value**
Intercept	20.70	1	66.52	<0.0001
Ration	2.79	2	4.48	0.01
Size	2.23	1	7.15	0.0086
Temperature	1.07	1	3.44	0.066
Residuals	33.92	109		

Chapter 6 – High site-fidelity and low mortality of juvenile Atlantic cod (*Gadus morhua*) in subarctic coastal habitat during their first winter

A version of this chapter was published as: Geissinger, E. A., Gregory, R. S., Laurel, B. J., and Snelgrove, P. V. R. 2022. High site-fidelity and low mortality of juvenile Atlantic cod (*Gadus morhua*) in subarctic coastal habitat during their first winter. ICES Journal of Marine Science, 79: 1408-1418.

Data were published as: Geissinger, E. A., Gregory, R. S., Laurel, B. J., and Snelgrove, P. V. R. 2021. Data for: High site-fidelity and low mortality of juvenile Atlantic cod (*Gadus morhua*) in subarctical coastal Newfoundland during their first winter. Scholars Portal Dataverse, V1, Available from https://doi.org/10.5683/SP3/NPQSLV.

6.1 Abstract

In subarctic Newfoundland, age-0 juvenile Atlantic cod (*Gadus morhua*) settle into coastal habitats in several summer and fall pulses, yielding a broad length-frequency distribution prior to their first winter. The first winter is often associated with physiological and metabolic stress and has been considered a critical survival period determining cohort strength. We evaluated size-structured overwinter mortality and movement using mark-recapture and condition metrics by marking 226 cod in two batches one week apart, in October 2016. We estimated fall and overwinter mortality, and documented movement of fish recaptured in May 2017 using Cormack-Jolly-Seber models. We recaptured 30 marked juveniles. High fall mortality characterized late settling cohorts relative to earlier settling cohorts ($16.6\%\cdot d^{-1}$ vs. $4.5\text{-}7.7\% \cdot d^{-1}$). Overwinter mortality was unexpectedly low (0.0052 and $0.0022\%\cdot d^{-1}$). Individual condition (Fulton's K) of juvenile cod remained high throughout winter across all size groups. We expected higher mortality of juvenile cod and broad dispersal of juveniles over winter (32-weeks). In contrast, our results indicated low mortality and high site-fidelity in their first winter. This study indicates the period leading up to winter is

important for survival, suggesting winter is not a survival bottleneck and may even provide a refuge compared to the rest of the year.

6.2 Introduction

Natural mortality at early life stages strongly influences recruitment potential. Natural mortality represents a critical defining variable in fish ecology and population dynamics, yet quantifying mortality is challenging in open, marine systems. Despite many gaps in current understanding of natural mortality, published evidence suggests that three main factors affect fish survival: size, growth rate, and ambient temperature (Pauly, 1980; Sewall *et al.*, 2019). Numerous studies have examined mortality rates for many species, from larval to adult stages (Peterson and Wroblewski, 1984; Gulland, 1987). Extensive research has considered natural mortality of Northeast Arctic cod (*Gadus morhua*) and European plaice (*Pleuronectes platessa*), providing an important baseline for juvenile population dynamics (Nash and Geffen, 2012; Ottersen *et al.*, 2014; Bogstad *et al.*, 2016). However, limited data availability on natural mortality rates in age-0 juveniles across regions and species continues to constrain our understanding of the relationship between early juvenile abundance and recruitment to fisheries.

Size-structured mortality dominates early life stages, particularly in juvenile fish in their first year of life (Sogard, 1997; Sewall *et al.*, 2019). The complex factors that influence size-structured mortality in age-0 juveniles involve the interplay of physiology and bottom-up processes (e.g., size-dependent energetics; Sogard and Olla, 2000) combined with behaviour and top-down processes (e.g., size-dependent movement and predation risk; Akimova *et al.*, 2019; MacRobert, 2020). Broadly speaking, large juvenile fish should have a survival advantage compared to small conspecifics because larger fish have more energy stores to endure periods of low productivity, reduced exposure to gape-limited predators ("predator window"; Cowan *et al.*, 1996; Beamish and Mahnken, 2001), improved swim-performance, and reduced need to forage in risky habitats (Heintz and Vollenweider, 2010; Sewall *et al.*, 2019). Numerous studies document size-dependent mortality across a wide range of fish species, recognizing that mortality may involve one or more of these processes (Sogard, 1997; Schindler, 2011).

Size-structured mortality may be especially important during winter. Research on Atlantic cod from the Barents Sea and haddock from the Barents Sea, the southern Scotian Shelf, and the Bay of Fundy shows a strong positive relationship between body size (length) at age-0 and abundance at age-1 (Stige *et al.*, 2019). In seasonal environments, highest rates of size-dependent mortality may occur in juveniles entering their first winter. Early spawning in sand smelt (*Atherina boyeri*) confers a survival advantage from their increased size at onset of winter, compared to later spawning individuals (Henderson *et al.*, 1988). Similarly, in bluefish (*Pomatomus saltatrix*), spring-spawned juveniles had higher survival than summer-spawned juveniles, although some of the latter group may also survive (Morley *et al.*, 2013). Juvenile rainbow trout (*Oncorhynchus mykiss*) rarely survive their first winter unless they achieve a critical size and energy threshold (Mogensen and Post, 2012). Similarly, age-0 pollock (*Gadus chalcogramma*) rarely survive their first winter following poor fall growth conditions (Heintz and Vollenweider, 2010). Yet, overwinter mortality and ecosystem dynamics during winter are poorly characterized for most species, especially in marine systems (Beamish and Mahnken, 2001; Hurst, 2007). Even in freshwater systems, where juvenile overwinter mortality has well-established links to year-class strength and poleward range (Post and Evans, 1989; Morley *et al.*, 2013), juvenile fish may actually experience lower mortality throughout winter compared to other times of the year. For example, Atlantic salmon (*Salmo salar*) parr experience higher initial mortality leading into winter compared to mid-winter when ice covers streams (Linnansaari and Cunjak, 2010). Additionally, size-dependent mortality during winter may not be evident when there is sufficient productivity (Geissinger *et al.*, 2021a). Therefore, overwintering mortality and size-dependent processes likely vary by species, region, and ecosystem.

Natural mortality rates in early life stages of cod have been difficult to characterize. Alteration in relative abundance of a cohort occurs sometime between egg production and the onset of their first winter (Campana, 1996; Bogstad *et al.*, 2016; Lunzmann-Cooke *et al.*, 2021). However, mortality rates for juveniles remain poorly studied due to size limitations for tagging and high mortality rates, necessitating the need to tag large numbers of individuals (Seber, 1982). Additionally, juvenile distributions are coarsely linked to dynamic seasonal and annual environmental conditions (Laurel *et al.*, 2017). Estimates of instantaneous mortality rates of Atlantic cod from Newfoundland range between 5.4 to 4.4% $\cdot$ y^{-1} from age 1 to age 3 (Anderson and Gregory, 2000), with reported daily instantaneous mortality rates of age-0 cod in Northeast Arctic cod (*G. morhua*) ranging from 0.005 to 0.021% $\cdot$ d^{-1} (Bogstad *et al.*, 2016). These estimates provide a starting point to understanding natural mortality in age-0 fish. However, poor understanding on the mechanisms and seasonal regulation of age-0 natural mortality for most marine fish species persist (i.e., size, energetics, predation, environment).

Reliable estimation of natural mortality requires understanding movement. One difficulty in estimating natural mortality is disentangling movement from mortality in fish populations (Pine *et al.*, 2003). We also know little on winter movement in age-0 marine fish. Few studies have characterized the distances travelled away from coastal habitats and movement patterns during winter (although see Shapeira *et al.*, 2014). In the Barents Sea, juvenile cod are relatively stationary until age-3 (Ottersen *et al.*, 1998). In the North Sea, pelagic juvenile cod (age-0 to -2) move inshore to shallow coastal nurseries during winter (Riley and Parnell, 1984). In contrast, juvenile cod (age-

1 to -2) in the Gulf of St. Lawrence move out of shallow coastal nurseries during winter to depths ranging between 100 and 200 m with the younger, smaller cod not migrating as far as the older juveniles (Hanson, 1996). These regional differences highlight the importance of understanding movement when estimating natural mortality.

In this study, we use capture-mark-recapture techniques and demographic information on cohorts (size, condition) to quantify overwintering mortality in age-0 Atlantic cod in coastal Newfoundland. Complementary otolith microchemistry analysis (trace elements) looked for evidence of changing habitat use over time. Trace elements, such as Mg, Ba, and Sr, capture temperature and salinity changes in marine fish (Elsdon and Gillanders, 2002) indicative of habitat and movement (Miller, 2011; Stanley *et al.*, 2016). Following settlement, age-0 cod in Newfoundland spend the summer and fall in or near eelgrass habitats (Gotceitas *et al.*, 1997; Grant and Brown, 1998; Laurel *et al.*, 2004), which provide cover from predators (Linehan *et al.*, 2001). Evidence suggests that juvenile cod do not move more than a few kilometers within a single season (Grant and Brown, 1998), but nonetheless mix and move at scales of ~100 m (Laurel *et al.*, 2004) in contiguous eelgrass meadows. Winter studies suggest juvenile cod likely use deeper water to avoid freezing (Methven and Bajdik, 1994; Grant and Brown, 1998), but their movement and mortality have not been quantified. Atlantic cod in Newfoundland are an excellent model species to test hypotheses of overwinter survival given their broad size distributions in the fall (Methven and Bajdik, 1994; Ings *et al.*, 2008). We hypothesize that 1) large individuals are more likely to survive their first winter compared to smaller individuals, and 2) juvenile cod randomly disperse among suitable habitats during their first winter after leaving coastal eelgrass habitats.

6.3 Methods

6.3.1 Study sites and fish sampling

Eelgrass habitat dominates the shoreline of Newman Sound, a fjord in Bonavista Bay, Newfoundland Canada, where we conducted our field work. We selected three sites within Newman Sound for this study: Newbridge Cove, Canning's Cove, and Mistaken Cove. In Newbridge Cove, a somewhat isolated, protected cove, eelgrass beds extend out to ~7 m depth. Canning's Cove is approximately 1.67 km across the sound from Newbridge Cove, and Mistaken Cove is located approximately 750 m east along the north coast of the sound (Fig. 6.1). We collected fish using a demersal seine net 25 m long and 2 m high, consisting of 19-mm stretched mesh. The beach seine can quantitatively sample juvenile cod as small as 30 mm standard length. We excluded fish smaller than 30 mm from our study because they are not considered fully settled. The net was deployed 55 m from the shore using a small open boat and retrieved by two individuals standing 16 m apart along the shore. The seine samples approximately 880 m^2 of habitat from the bottom substrate to 2 m into the water column with a capture efficiency of approximately 95% (Gotceitas *et al.*, 1997).

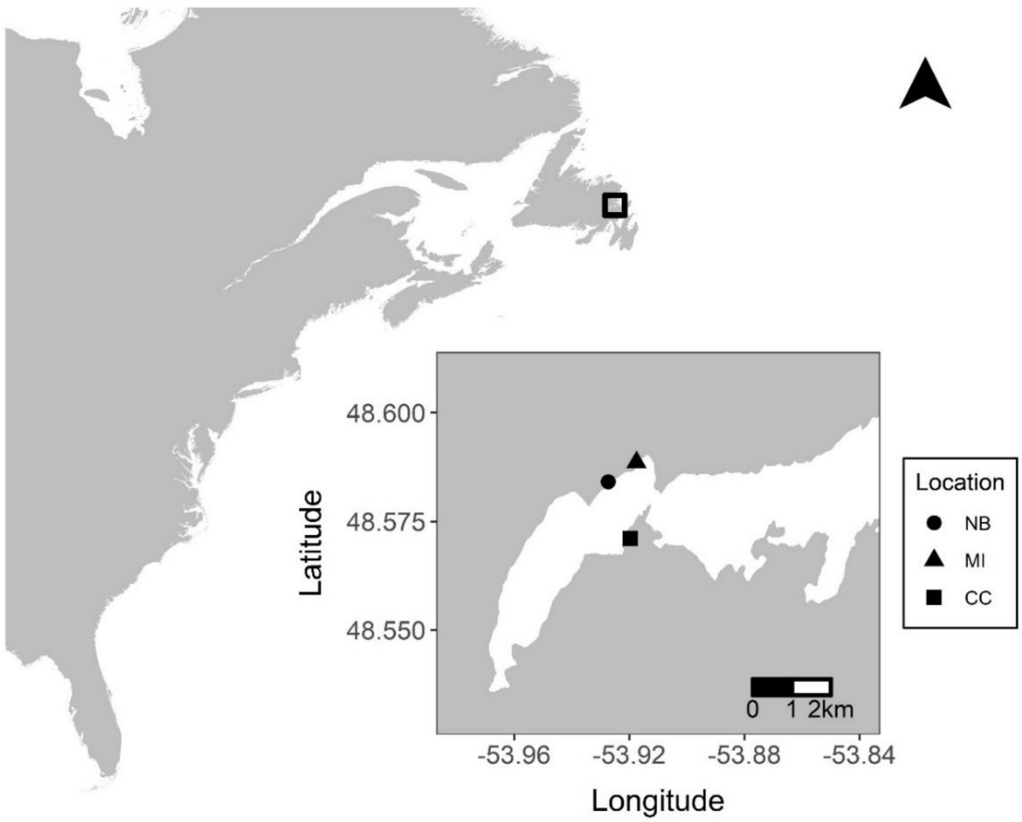


Figure 6.1. Newman Sound, Newfoundland in the context of eastern North America, showing fish sampling locations in October 2016 and May 2017 (circle, Newbridge Cove; triangle, Mistaken Cove; square, Canning's Cove).

We assigned sampled fish into recruitment pulses (see Ings *et al.*, 2008) using size-frequency distributions and finite mixture distribution models (Macdonald and Du, 2018) in the R programming language (R Core Team, 2021). Pulse assignments were derived from the Newman Sound long-term monitoring program from Fisheries and Oceans Canada. A biweekly sampling program enables detection of new pulses by tracking the growth of each pulse over time and thus detection of new pulses in the population (Methven and Bajdik, 1994; Ings *et al.*, 2008). We use finite mixture distribution models to determine the size-class distributions for each sampling trip, and then assign the pulses based on growth trajectories over the course of the season (Chapter 3; Gregory *et al.*, 2019).

6.3.2 Marking technique

We applied fluorochrome markers – calcein (Sigma-Aldrich: C0875-25G) or alizarin red S (Sigma-Aldrich: A5533-25G) – to batch mark otoliths (Lü *et al.*, 2020). Fluorochrome dyes bind with calcium in the otolith and, while exposed to the dye, fish lay down a distinct mark in the daily growth rings that can be read with confidence after recapture (Schmitt, 1982; Campana and Neilson, 1985). We marked age-0 juvenile cod in our study by immersing them for 24 h (Schmitt, 1982). Calcein fluoresces yellow and alizarin red S fluoresces red. This method produces a persistent mark that minimizes detrimental tagging effects induced by other common external tagging methods – e.g., fin clipping or externally visible markings (e.g., tattoos, brands, or various manufactured tags). We conducted validation trials to establish tag retention at effective and non-toxic concentrations. Validation trials focused predominantly on juvenile Greenland cod (*Gadus macrocephalus ogac*) because of availability of fish at an appropriate size at sampling. We further validated marks on Atlantic cod throughout the marking period by confirming application of marks on the subsampled fish (See Appendix 6.1). Although we confirmed 100% tag retention, observer effort nonetheless added a risk of tag-loss. To minimize tag-loss from observation, we analysed both sagittal otoliths from each sampled fish.

6.3.3 Mark-recapture

We set up tanks at Salton's Marine Interpretation Centre in Terra Nova National Park, near our capture-release site to mark fish for our mark-recapture experiment. We placed two 80-L treatment aquaria inside 120-L plastic water baths with a flow-through water source to maintain ambient temperature (10.4-11.4° C). Temperature, dissolved oxygen, and pH were monitored regularly throughout the 24-hour marking period. Fluorochrome can decrease pH levels; therefore, we maintained a consistent pH level using Na_2CO_3. Fluorochrome solutions were prepared as a stock solution, which we slowly added into the tanks.

We collected age-0 Atlantic cod from Newbridge Cove (Fig. 6.1) in 5-6 beach seine hauls on each of October 13, 14, and 18, in 2016. We measured a random subsample (n=51 on 13 October; n=30 on 18 October) of cod to the nearest mm Standard Length (mmSL; snout to the caudal peduncle) from each date to determine size distribution of individuals captured. We captured 184 age-0 juvenile cod in seine hauls on 13 and 14 October and held them in calcein (50 $mg \cdot L^{-1}$) treatment aquaria. A total of 6 juvenile cod mortalities occurred during the marking period, which we attributed to handling stress prior to the treatment. Mortalities were sampled to validate mark retention. On 15 October, we released 178 of these marked fish at the capture-release site. We observed no evidence of mark-induced mortality among 30 marked individuals we held in a submerged 40-L cage at our study site for one hour prior to release.

We captured another 149 juvenile cod on 18 October and held them in alizarin red S baths (250 $mg \cdot L^{-1}$) for 24 h, prior to releasing a total of 129 fish into Newbridge Cove on 19 October. Twenty fish did not survive the overnight marking treatment; however, again, we observed no additional mark-induced mortality among 30 individuals we held at our study site for one hour prior to release; in our experience, most mortalities occur relatively quickly after marking and prolonged holding times beyond one hour can add additional handling stress.

We captured marked and unmarked age-1 Atlantic cod on 24 and 25 May 2017 using the same seining technique, at the release cove and at two nearby coves – 289 cod at Newbridge Cove (capture-release-recapture), 50 cod at Canning's Cove (recapture), and 62 cod at Mistaken Cove (recapture). We conducted two seine hauls at Newbridge Cove, three at Canning's Cove, and one at Mistaken Cove. These fish were frozen at -10 °C on site, then transported to the laboratory and stored frozen until we could examine their otoliths for marks. We calculated catch per haul across Newman Sound for the first marking period (14 October 2016) and recapture period (25 May 2017).

The juvenile cod sampled in May then formed the basis for our capture-mark-recapture analysis (see details below). Recapture rates could not be calculated from the October marking periods, since the fluorescent marks were internal. Therefore, the fall recapture rate is dependent on marked fish surviving winter. Research was conducted under Memorial University of Newfoundland and Labrador Animal Care protocol #16-02-RG.

6.3.4 Otolith analysis

For all fish captured in May 2017, we measured standard length and extracted sagittal and lapillus otoliths. Sagitta were mounted, sulcus facing upwards, on slides using Crystal Bond™. Sagittal otoliths were ground on the longitudinal plane using 15 µm finishing film and polished with 3 µm lapping film. We then viewed the otoliths for potential marks using a Zeiss Axio Imager A1™, 10x/23 eye and 10x/0.3 objective lenses. The microscope was fitted with an AmScope Microscope Digital Camera™ (MU1203-FL). We examined otoliths for calcein marks using a filter that excites at 450-490 nm wavelengths, allows emission at 515 nm, and has a beam splitter at 510 nm. Alizarin red S was viewed using an alizarin red S filter set (Chroma Technology™) that excites at 510-560 nm with a 590 nm barrier filter.

6.3.5 Sample preparation for trace elements

To provide inference on environmental histories in recaptured juvenile cod, we selected a subsample of 60 otoliths from our May 2017 recaptures for trace element analysis using secondary ion mass spectrometry (SIMS). Through this analysis, we aimed to determine whether juvenile cod move to deep, isothermal water. Cod that move to deep water, would show minimal trace element variation among fish, and Mg levels would decrease from the fall band to the winter band (Stanley *et al.*, 2015). A Cameca IMS 4f Secondary Mass Spectrometer was used to perform spot analysis of Na/Ca, Mg/Ca, Sr/Ca and Ba/Ca in the fall and winter growth bands of otoliths. The fall and winter bands were traced based on visual assessment. We selected marked and unmarked individuals from two size groups – large (99-132 mm SL; Pulse 1) and small (71-96 mm SL; Pulse 2) individuals. The large size group contained 4 marked and 15 unmarked individuals, whereas the small size group included 14 marked and 27 unmarked individuals. Given the limited information on trace element levels in relation to temperature in juvenile cod, we sampled cross sections, from the edge of the otolith to the core, of an additional four otoliths from a previous experimental study (Geissinger *et al.*, 2021a) to provide a limited comparison between field caught juveniles, and those with a known winter temperature profile (See Appendix 6.3). We sectioned sagittal otoliths with a thin kerf Beuhler Isomet™ low speed saw and hand polished them to the core before mounting otolith sections into a SIMS sample ring (aluminum ring with 25.4 mm outside diameter) and embedding them in the ring using epoxy resin. Polishing the casts and SIMS analyses followed the methods of Aranha *et al*. (2014). Otolith elemental compositions were converted to molar values and standardized to calcium concentrations (Me:Ca). Trace element analysis for this study has unknown predictive power given it is used in a small-scale winter marine coastal environment (Stanley *et al.*, 2016).

6.3.6 Statistical analysis

We ran capture-mark-recapture models with Cormack-Jolly-Seber formulation using the programs MARK (version 9.0) and RMark (Laake, 2013). These models allowed us to calculate period-specific apparent survival rates. Survival rates, φ_i, denote the probability of survival from release occasion i to release occasion $i+1$. Recapture probability, p_i, describes the probability of capture or recapture on occasion i. We ran 8 models with φ and p under different constraints: constant (φ, p), varying with time (φ, p), and varying with size (φ), and chose the top model, using Akaike Information Criteria (AIC). We calculated the overdispersion parameter, ĉ, by dividing the observed ĉ from the model by the mean ĉ from simulations; we considered a ĉ value greater than 1 meant over dispersed.

Daily natural mortality (M) is reported as % per day using the formula:

$$M = ((1 - \varphi) \cdot \mathrm{d}^{-1}) \cdot 100. \tag{1}$$

The marking period (d) for the fall sample was 6 days (13-19 October 2016), and the marking period for the overwinter period was 223 days (19 October 2016 – 24 May 2017). We calculated condition of captured fish in May (marked and unmarked) using Fulton's K condition factor (Fulton, 1904; Grant and Brown, 1999), with dry weight as:

$$K_{DRY} = 1000 \cdot (\mathrm{W}_{\mathrm{DRY}} \cdot \mathrm{L}^{-3}), \tag{2}$$

and with W_{DRY} as dry eviscerated weight (g) and L as standard length (cm). We calculated hepatosomatic index (HSI, Lambert and Dutil, 1997) as:

$$HSI_{DRY} = 1000 \cdot (LW_{DRY} \cdot W_{DRY}^{-1}), \tag{3}$$

with LW_{DRY} as dry liver weight (g). We analysed condition and HSI using a generalised linear model, with a gamma distribution to determine whether condition changed between size class (pulse) or sampling location post-winter. The models used Fulton's K and HSI as response variables, respectively, with pulse and location (Newbridge, Canning's, or Mistaken) as fixed explanatory variables (categorical). The models included an interactive effect between pulse and location, but the interactive effect was removed when $p \geq 0.05$.

Trace element (Mg, Ba, Sr) analysis used a generalised linear mixed effect model with a gamma distribution and log link. Pulse, season, and location were fixed explanatory variables, and otolith ID was a random effect. All statistical analyses were conducted using R statistical programming language (R Core Team, 2021). Associated data are available on Scholars Portal Dataverse (Geissinger *et al.*, 2021b).

6.4 Results

6.4.1 Initial size distribution

Size distribution from the subsample (n = 51) ranged from 41-84 mm SL during our first marking period on 14 October 2016. The marked population contained three settlement pulses – Pulse 1 (n = 39) ranged 66 - 84 mm SL (76.0 ± 5.9, mean ± s.d.), Pulse 2 (n = 46) ranged 46 - 65 mm SL (58.3 ± 5.5), and Pulse 3 (n =3) contained one size at 41 mm SL. (Fig. 6.2a). On 19 October, subsampled (n = 30) size distribution ranged 52 - 93 mm SL: Pulse 1 (n = 24) ranged 68 - 93 mm SL (79.4 ± 8.0) and Pulse 2 (n = 52) ranged 52 - 67 mm SL (61.7 ± 4.4; Fig. 6.2b).

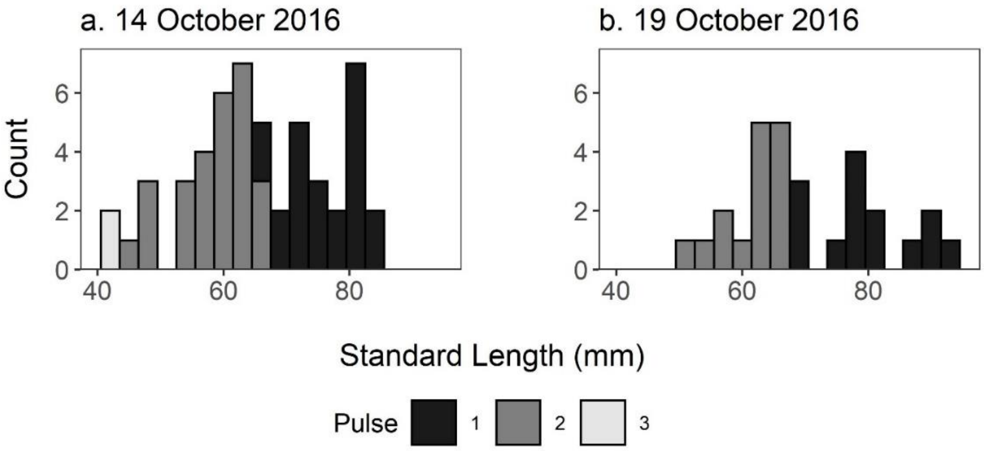


Figure 6.2. Size distribution of subsampled age-0 Atlantic cod caught on (a) 14 October 2016 (n=51) and (b) 19 October 2016 (n=39). Shading represents pulse assignment for each size-class.

6.4.2 Recaptures

We captured a total of 281 cod on 24 May 24, 2017, at our Newbridge Cove release site and the two nearby sites (Fig 6.1). We captured 103 Pulse 1 fish ranging 98 - 151 mm SL (114.0 ± 11.0) and 156 Pulse 2 fish ranging 69 - 97 mm SL (81.2 ± 8.5). There were 7 Pulse 3 ranging from 62-68 mm SL (64.9 ± 2.3). Additionally, we captured 15 individuals from Pulse 4, which ranged 41 - 60 mm SL (49.7 ± 7.0; Fig. 6.3a); we captured no Pulse 4 individuals in Newbridge Cove in October 2016 because these fish had yet to settle into our study site when we began our marking experiment. Therefore, we excluded all Pulse 4 fish captured in May from CMR analysis. The size distribution at Mistaken Cove ranged 32 - 109 mm SL, including elements of Pulse 1 (106 - 109 mm SL; n = 2), Pulse 2 (69 - 96 mm SL; n = 17), Pulse 3 (62 - 67 mm SL; n = 6), and Pulse 4 (32-61 mm SL; n = 37; Figure 6.3b). At Canning’s Cove, Pulse 1 ranged 99 - 132 mm SL (n = 8), Pulse 2 ranged 75 - 97 mm SL (n = 29), Pulse 3 ranged 63 – 66 (n = 2), and Pulse 4 ranged 41 - 55 mm SL (n = 11; Fig. 6.3c).

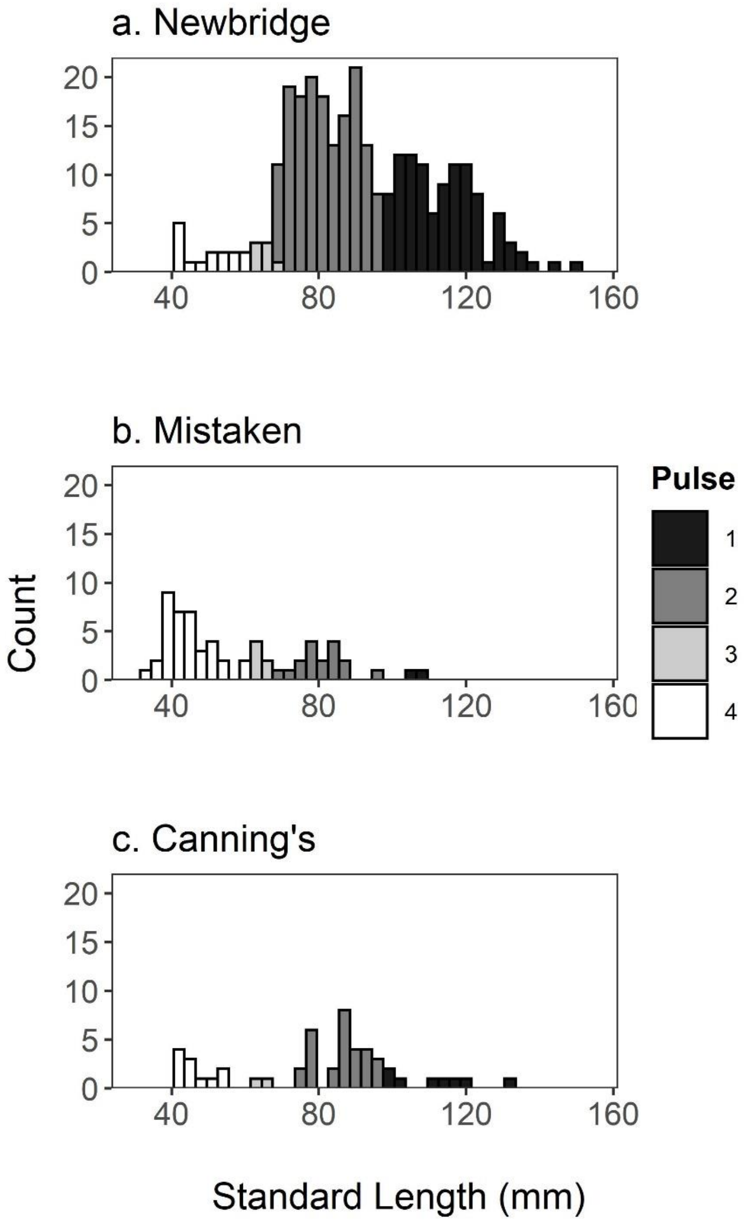


Figure 6.3. Size distribution histograms of age-1 Atlantic cod caught on 24 May 2017, from (a) Newbridge Cove, (b) Mistaken Cove, and (c) Canning's Cove. Shading represents pulse assignment for each size class.

We recaptured a total of 33 marked juvenile cod in May 2017, 32 weeks after initial marking the previous fall. The majority of marked juvenile cod we recaptured (30 individuals) were taken at our Newbridge Cove marking site, including five cod from the first marking period (14 Oct), 24 cod from the second marking period (19 Oct), and one double-marked individual (exhibiting both a calcein and an alizarin red S mark; Fig. 6.4). At this site, three recaptures were from Pulse 1, with the remainder (27) from Pulse 2. The three recaptures at Mistaken Cove (a recapture site only) all came from the 14 Oct marking period and they were from Pulse 2; we observed no individuals from the 19 Oct marking at this site. There were no recaptures from Canning's (a recapture site only).

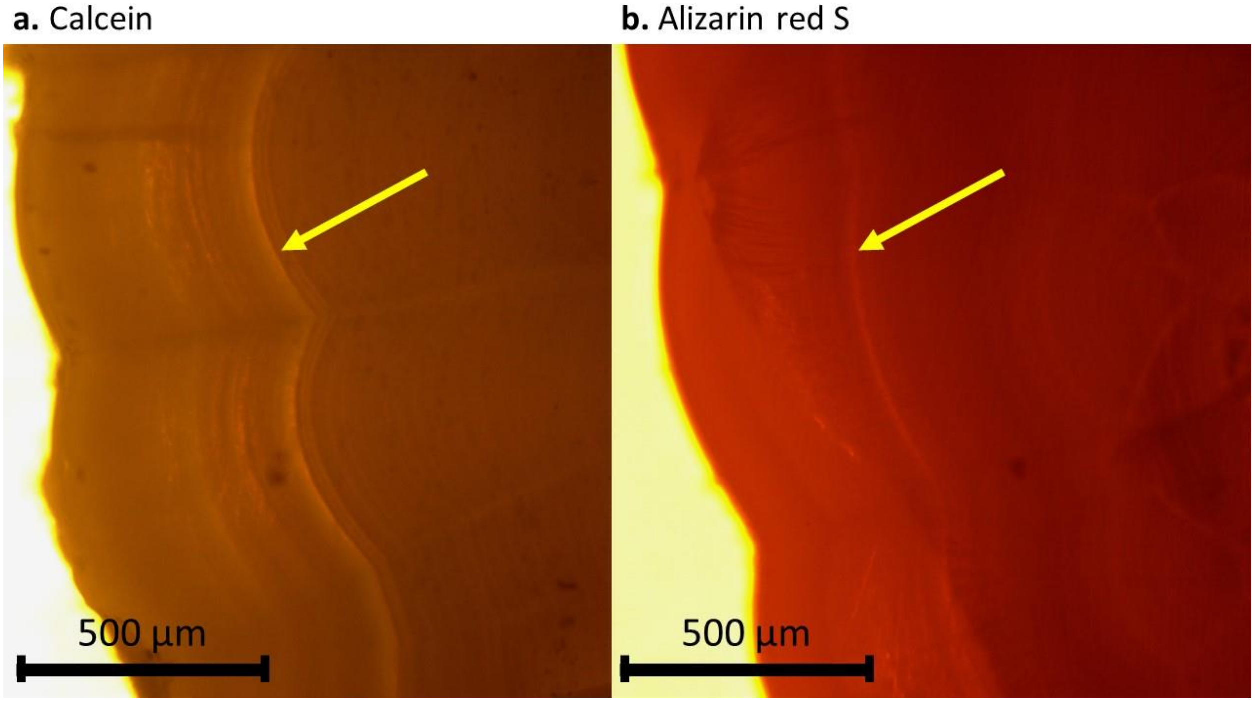


Figure 6.4. Sagittal otoliths from two mark-recaptured juvenile Atlantic cod (*Gadus morhua*) (May 2017), initially marked and released with (a) calcein (14-15 October 2016) and (b) alizarin red S (19 October 2016).

6.4.3 Condition

A generalised linear model showed that the interaction between pulse and site significantly influenced Fulton's K condition factor, K_{DRY} (ANODEV; χ^2=25.71; df=6,381; p<0.001). Pulse 1 fish at Mistaken Cove, which had an average K = 2.13 ± 0.41, likely drove the interaction between site and pulse. Mean values of all other pulses and sites ranged between 1.57 and 1.86 (Fig. 6.5a).

HSI varied with pulse (ANODEV; χ^2=57.28; df=3,372; p<0.001), but not site (ANODEV; χ^2=0.38; df=2,372; p=0.83). Pulse 1 HSI averaged 1.46 ± 0.40 compared to 1.43 ± 0.41 for Pulse 2. Pulse 3 HSI (1.19 ± 0.46) and Pulse 4 HSI (0.94 ± 0.41) were significantly lower than Pulse 1 and Pulse 2 (Fig. 6.5b).

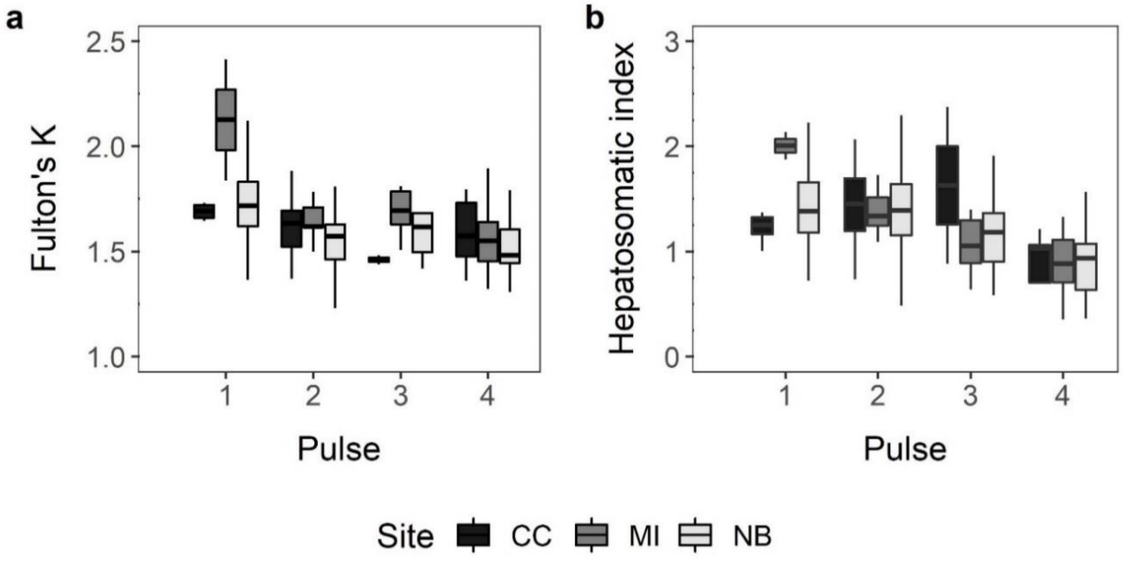


Figure 6.5. Fulton's condition factor, K_{DRY} (a) and hepatosomatic index (HSI) for age-1 Atlantic cod collected in Newman Sound on 24 May 2017. Fulton's K had a significant interaction between site (CC: Canning's Cove; MI: Mistaken Cove; NB: Newbridge Cove) and pulse (ANODEV; χ^2 = 22.76; df = 4,377; p < 0.001). HSI differed significantly between pulses (ANODEV; χ^2 = 56.44; df = 2,366; p < 0.0001). The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range.

6.4.4 Capture-mark-recapture models

Given the low recapture rates at neighbouring sites, we only modeled marked and recaptured cod at Newbridge Cove, acknowledging the limitations associated with evidence of post-winter migration of marked fish after 32 weeks at large. The best-fit model was φ(time*pulse) and p(time) with AIC = 166.26. A bootstrap goodness-of-fit with 1000 simulations showed reasonable likelihood of the observed model deviance of 4.96, with 124 of the simulated values exceeding the observed value (p = 0.123). The model ĉ = 4.96 indicates slight over-dispersion.

Mortality rate varied by pulse and time, and recapture probability varied with time (Table 6.1). Pulse 1 mortality M = 7.71% $\cdot$ d^{-1} (± 1.6% $\cdot$ d^{-1} se) in the October 2016 sampling strongly contrasted M = 0.00515 % $\cdot$ d^{-1}(±0.001) over the 32-week period at-large (over winter). Pulse 2 mortality M = 4.52% $\cdot$ d^{-1} (±0.99) in the October sampling period greatly exceeded M = 0.0022 % $\cdot$ d^{-1} (±0.0003) over winter. In contrast, we observed higher Pulse 3 mortality in October of M = 16.63% $\cdot$ d^{-1} relative to the other pulses, but overwinter mortality consistent with the first two pulses with M = 0.39% $\cdot$ d^{-1}. However, small sample size resulted in low precision and high error for Pulse 3 estimates during both time periods (Table 6.1). Lower sample size in the initial marking period characterized juvenile cod from Pulse 3 along with low abundance during our sampling in May 2017. Catch per haul for Pulse 1 in Newman Sound of 31.9 cod $\cdot$ $haul^{-1}$ on 14 October 2016 contrasted 7.3 cod $\cdot$ $haul^{-1}$ on 24 May 2017. We collected 11.6 cod $\cdot$ $haul^{-1}$ in October 2016 and 16.9 cod $\cdot$ $haul^{-1}$ in May 2017 from Pulse 2. Lastly, there were 0.4 cod $\cdot$ $haul^{-1}$ in Pulse 3 in October 2016 and 0.0 cod $\cdot$ $haul^{-1}$ in May 2017.

Table 6.1. Cormack-Jolly-Seber (CJS) model output for Newbridge Cove (N=249), specified as: φ(~time + pulse)p(~time), with the marking/recapture period, estimate as the apparent survival probability (φ) and apparent capture probability (p), and standard error (se), 95% lower confidence limits (lcl) and 95% upper confidence limits (ucl).

Parameter	**Pulse**	**Marking/recapture period**	**Estimate (survival · period^{-1})**	**se**	**lcl**	**ucl**
Φ	1	Fall (1 week)	0.54	0.094	0.36	0.71
Φ	1	Winter (32 weeks)	0.99	0.0022	0.98	0.99
Φ	2	Fall (1 week)	0.73	0.060	0.60	0.83
Φ	2	Winter (32 weeks)	0.99	$0.76\text{x}10^{-3}$	0.993	0.996
Φ	3	Fall (1 week)	0.0022	40.23	0.00	1.00
Φ	3	Winter (32 weeks)	0.14	2210.12	0.00	1.00
P	1; 2; 3	Fall (1 week)	0.054	0.057	0.0063	0.34
P	1; 2; 3	Winter (32 weeks)	1.00	$1.64\text{x}10^{4}$	0.00	1.00

6.4.5 Trace elements

Trace elements (Mg, Ba, Sr) did not vary significantly by pulse or site (p>0.05; Appendix 6.4 – 6.6). Mg and Ba values both differed significantly among field fish between fall and winter (Mg: ANODEV, χ^2= 35.28; df = 1,124, p < 0.01; Fig. 6.6), with an increase in mean Mg from 0.131 ± 0.009 mmol (mean ± se) in the fall to 0.166 ± 0.011 mmol in the winter. Standard deviation of Mg in the winter (0.071 – 0.662 mmol) was twice that in fall (0.071 – 0.294 mmol, Table 2). Ba differed significantly between fall and winter (ANODEV, χ^2= 24.549; df = 1,124, p < 0.01), with a mean increase from 0.0021 ± 0.00013 mmol in the fall to 0.0026 ± 0.00016 mmol in the winter. Sr values did not differ significantly among field fish between fall and winter (ANODEV,

χ^2= 3.21; df = 1,124, p=0.07). Ba, Sr, and Mg cross sections from 4 individual cod from a controlled lab experiment did not vary substantially (Appendix 6.3). The winter temperatures at our sites in 2016-2017 ranged from -1.3 to 5.3 °C overwinter (1 December 2016 – 24 May 2017), whereas the temperature experienced by the control fish ranged from -0.7 to 3.1 °C.

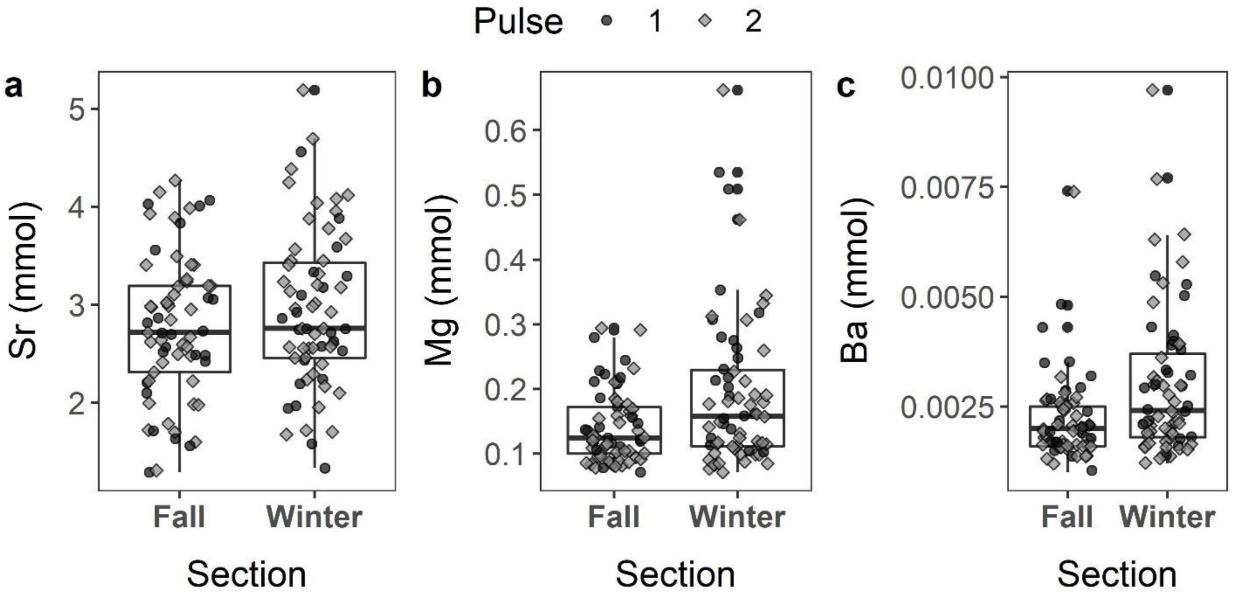


Figure 6.6. Trace element (a: Sr, b: Mg, c: Ba) of age-1 juvenile Atlantic cod sagittal otoliths on the fall and winter bands (n=60). No differences were detected between pulses. The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Points represent individual measurements for each fish.

Table 6.2. Trace elements for age-0 Atlantic cod sagittal otoliths (N=60) including fall and winter measurements with means, standard deviations (SD) and ranges (min-max).

Trace element	**Section**	**Mean (mmol)**	**SD (mmol)**	**Range (mmol)**
Sr	Fall	2.77	0.741	1.29 – 4.27
	Winter	2.97	0.790	1.33 – 5.19
Ba	Fall	$2.21 \cdot 10^{-03}$	$9.62 \cdot 10^{-04}$	$1.00 \cdot 10^{-03}$ - $7.40 \cdot 10^{-03}$
	Winter	$2.88 \cdot 10^{-03}$	$1.44 \cdot 10^{-03}$	$1.20 \cdot 10^{-03}$ - $7.70 \cdot 10^{-03}$
Mg	Fall	0.14	0.0559	0.071 – 0.290
	Winter	0.19	0.1180	0.071 – 0.660

6.5 Discussion

Past studies point to the overwinter period as a significant survival bottleneck for both freshwater and marine species (Henderson *et al.*, 1988; Garvey *et al.*, 1998; Ellis *et al.*, 2017). Despite strong evidence for this bottleneck, the factors driving winter survival remain inconclusive. Some studies support energetic-based mortality (Norcross *et al.*, 2001) whereas others support predation-based mortality (Cowan *et al.*, 1996). The observed low mortality – $0.005\% \cdot d^{-1}$ or less for the largest juveniles in their first winter indicates that winter does not cause a significant survival bottleneck for young-of-the year cod in Newfoundland.

This overwinter mark-recapture study provides the first information on juvenile overwinter mortality and habitat use for cod *in situ*. Our results do not support our first hypothesis that the size of juvenile fish entering winter is an important component of overwinter mortality. We observed lower mortality in the first two settlement pulses (i.e., largest individuals) compared to the smaller third pulse fish, which arrived in our coastal site in mid-October. However, winter mortality was also low for the third pulse (0.39% · d^{-1}), but our limited sample size for Pulse 3 cod limits our confidence in the Pulse 3 mortality estimate. Our results indicate that 60+ mm cod in the fall have a distinct survival advantage over the 50-58 mm cod arriving later in the fall. The third settlement pulse had high mortality in the fall, with few Pulse 3 fish detected in Newman Sound in the spring or summer. Additionally, a fourth pulse (~30-60 mm in the spring) appeared in our nearshore sites after November 2016 and maintained unexpectedly high abundances through May 2017 (Gregory *et al.*, 2019). The high representation of a fourth settlement pulse further supports our assertion that small size does not limit overwinter survival in our study area. However, we do not know the initial abundance of Pulse 4, which limits our full understanding of their survival.

Energetics impacts overwinter mortality in many freshwater and marine juvenile fishes (Sogard and Olla, 2000; Heintz and Vollenweider, 2010; Mogensen and Post, 2012). Harsh winter conditions can often intensify size-structured mortality in fishes due to cold temperatures and food limitation (Fullerton *et al.*, 2000; Huss *et al.*, 2008). Freshwater studies show substantial starvation mortality during winter (e.g., Post and Evans, 1989), where mortality regulators include size, food availability (Garvey *et al.*, 1998), and winter severity – i.e., duration, photoperiod, and temperature (Fullerton *et al.*, 2000). Winter mortality rates as low as 0% characterize warm, high resource freshwater environments, in contrast to 18% in warm winters with low resource abundance (Mogensen and Post, 2012). However, in cold lakes, when size and lipid availability in fish fall below threshold levels, mortality levels increase to 94% (Mogensen and Post, 2012). Studies of marine systems yield similar results. For example, sand smelt (*Atherina boyeri*) showed almost 50% mortality in two consecutive winters (Henderson *et al.*, 1988). Additionally, low winter temperatures impact temperate systems in the most severe winters, where marine fish (*Micropogonias undulatus*; *Cynoscion nebulosus*) cannot tolerate low temperatures (Lankford and Targett, 2001; Ellis *et al.*, 2017). However, low temperatures do not always have a negative effect. Increased condition and growth can occur in northern latitude species, such as Pacific herring (*Clupea pallasii*) during cold years (Sewall *et al.*, 2019). In contrast to Atlantic cod and herring, extreme winter temperatures in temperate regions lead to "winterkills", that expose fish to lethal thermal conditions (Ellis *et al.*, 2017), sometimes caused by osmoregulatory failures (Johnson and Evans, 1996). Thus, our finding of low mortality in juvenile cod contrast our initial expectations as well as some published findings for freshwater and temperate marine species.

Based on experimental studies of Fulton's K condition, juvenile Atlantic cod remained in relatively high condition post-winter in our study, averaging 1.5 or greater for all pulses and locations. Fulton's K (dry) condition factor can vary from ~1.0 for juvenile cod under starvation conditions, and ~1.5 when food exceeds 5% body weight per day (Geissinger *et al.*, 2021a). Therefore, the Fulton's K data suggest age-0 cod were likely not energy limited during winter. However, the HSI condition metric varied with size of fish, with Pulse 1 and 2 values of ~1.4, and Pulse 4 values less than 1.0. This distinct change in HSI between size groups indicates either: 1) larger juveniles accumulate more relative liver energy pre-winter (either through foraging opportunity or size-dependent energy allocation), or 2) smaller juveniles consume more energy stores in the liver during winter. Testing these hypotheses will require further studies, although our data suggest winter survival was neither size-dependent nor overly impacted by energy limitation in the winter of 2016-17.

Atlantic cod possess physiological adaptations to minimize the impact of low winter temperatures. Increased concentrations of antifreeze glycoproteins in juvenile Atlantic cod entering the winter period allow them to endure sub-zero temperatures (Fletcher *et al.*, 1987). Nevertheless, we had expected high mortality overwinter in age-0 cod, given our *a priori* perception of limited resources and low mean temperatures during this period. We had anticipated that low productivity in the coastal zone during the winter period (Foy and Paul, 2004) would have led to depleted energy stores in juveniles, increasing metabolic stress and increasing mortality over winter. Geissinger *et al.* (2021a) showed that age-0 Atlantic cod can survive and grow in low temperatures (-0.8 to 2.7 °C) assuming availability of at least some food. Low mortality rate and high condition indices of overwintering juvenile cod suggest that the juveniles in our study may have had sufficient access to food throughout the winter (Geissinger *et al.*, 2021a), although we did not expect this outcome given published accounts of winter zooplankton availability in Newfoundland (Wilson *et al.*, 2018).

A critical size threshold can be challenging to measure during overwinter periods (Beamish and Mahnken, 2001). Winter mortality rates alone do not demonstrate size-structured predation *per se*. However, using our fall capture-mark-recapture period, we infer the unexpected presence of a "predator window" prior to winter. Pulse 3 fish were estimated to experience high mortality in the late fall ($16.63\% \cdot d^{-1}$), which suggests that Pulse 3 cod did not likely survive to the start of winter. Pulse 3 mortality rates require cautious interpretation given the small sample size. We attribute this high fall mortality to predation based on two lines of evidence. First, emigration is unlikely a factor based on a concurrent study in the system that showed juvenile cod limit movement to similar habitats (MacRobert, 2020). Secondly, we predict that predators likely consumed the Pulse 3 fish prior to winter while ambient conditions remained comparatively warm and metabolic demands and foraging activity were presumably higher. Pulse 1 and Pulse 2 fish survived to the start of winter, possibly due to their ability to evade predators or outgrow the size that predators can capture them (Schmitt and Holbrook, 1984; Persson *et al.*, 1996). Examples of predators in this system are cunner (*Tautogolabrus adspersus*) sculpin (*Myoxocephalus scorpius*), age 1-2 cod (*G. morhua; G. ogac*) and white hake (*Urophycis tenuis*; Linehan *et al.* 2001). High abundances of age 1 cod (2015 cohort) at our study site persisted throughout the fall in 2016, only relocating away from shore into winter habitat in late November in 2016 (Gregory *et al.*, 2019), after we had deployed our marks.

We offer two complementary hypotheses to explain why mortality was lower than expected in age-0 cod facing their first winter in coastal Newfoundland. First, predators in the area likely overwinter in deeper, warmer habitats to reduce risk of freezing, whereas age-0 juveniles produce sufficient antifreeze glycoprotein to remain in the nearshore and survive sub-zero temperatures (Fletcher *et al.*, 1987). Secondly, juvenile cod may also reduce their encounter rates with predators by restricting movement and occupying structured 'refuge' habitats typically found in the nearshore e.g., kelp, eelgrass (e.g., Gregory and Anderson, 1997). This age-0 overwintering strategy would also explain the high site fidelity in the nearshore observed in our study. Laurel *et al.* (2004) and Ryan *et al.* (2012) indicate that juvenile cod indeed move among neighboring eelgrass patches within a limited area. Our evidence supports overall high site fidelity overwinter. Had juvenile cod exhibited random dispersal behaviour, marked fish would have dispersed broadly to numerous locations along the shore of the sound. In such a scenario, recapture of any juveniles in the post-winter period (May) at our mark-release site would have been unlikely given the availability of suitable habitat in the immediate study area. In contrast, the large number of recaptures (~15%) strongly suggests that juvenile cod remain close to their pre-winter habitat overwinter, possibly due to reduced swimming activity related to cold temperatures (Laurel *et al.*, 2016). Alternatively, juvenile cod could be active during the winter period, similar to age-1

Greenland cod who have a larger home range in the winter relative to other seasons (Shapiera *et al.*, 2014). In this scenario, juvenile Atlantic cod would actively return to their settlement sites, further supporting strong site-fidelity.

The trace element analysis of otoliths did not provide conclusive insight into the environmental histories of mark-recaptured juvenile cod. Although non-significant discrimination among samples analysed by trace elements is inconclusive, we report results as they will be valuable for future studies using these tools at different scales, seasons and ontogenetic stages. The high variation in Mg levels in the winter section of otoliths, along with overlap in Mg values in the fall sections, defied our expectations. Based on an experimental study on the impacts of temperature and salinity on trace elements in juvenile Atlantic cod, Stanley *et al.* (2015) showed decreased Mg:Ca ratios in otoliths with decreased temperature. Instead of an overall decrease in Mg levels in the winter compared to the fall, we observed high variation and strong overlap between the two time periods. If we assume a clear trace element signal, then this observation suggests two potential scenarios. Juveniles either: 1) do not overwinter in the same location, or 2) remain close to shore, in shallow water with greater thermal variation relative to deep water. However, we cannot draw firm conclusions from these data because trace element incorporation in otoliths has not been verified in field studies for Atlantic cod, and temperature and salinity both impact incorporation rates (Miller, 2011). Juvenile cod presumably remain close to their settlement sites, and do not move to deep water for thermal refuge. Instead, they remain close to the coast where they experience large temperature changes associated with oceanographic processes. Few published studies address juvenile overwinter movements in marine ecosystems (however, see Hanson, 1996; Gregory and Anderson, 1997: Shapiera *et al.*, 2014). Although we do not know how far they move, our collective data indicate that age-0 cod make microhabitat shifts pre-winter (i.e., depart eelgrass beds) but likely exhibit little movement during winter.

6.6 Conclusions

Age-0 fish in sub-arctic marine ecosystems experience unique physical and physiological challenges compared to those in temperate waters. Length and severity of winter certainly contribute to these challenges. The northern population of Atlantic cod in Canada has not recovered since the fisheries moratorium first declared three decades ago through to the time when we conducted this study (DFO, 2019). The transition from age-0 to age-1 has remained poorly understood in the context of population assessment (e.g., Boudreau *et al.*, 2017; Rose and Walters, 2019), with little specific focus on the overwinter period. Contrary to previous studies, especially in freshwater ecosystems, the winter period does not appear to be a major source of additional mortality following settlement in the first year of life. This study provides important insight into overwinter dynamics seldom investigated in marine environments. Determining whether these seasonal conditions broadly represent a longer time series will require further studies.

Critical periods can provide information on recruitment patterns and vulnerable phases of early-life histories of juvenile fishes. Age-0 cod are important in determining juvenile cod year class strength, especially for weak year classes (Lunzmann-Cooke *et al.*, 2021) Therefore, understanding mortality from age-0 to age-1 can clarify the relationship between pre-recruits and adult populations. Our study indicates late fall may be a critical period which needs to be considered in recruitment processes for cod, and that winter mortality may be significantly lower than other times of the year.

6.7 Acknowledgements

This research was sponsored by the Natural Sciences and Engineering Research Council of Canada through the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada (including Productive Capacity and Marine Conservation Targets programs) and INREST (representing the Port of Sept-Îles and City of Sept-Îles, Quebec). We would like to also thank Parks Canada (Terra Nova National Park) for providing access to facilities, and the Department of Fisheries and Oceans for accommodations and field assistance. We offer a special thanks to K. Dalley, B. Newton, S. Anderson, C. Bloom, E. MacRobert, and E. Lunzmann-Cooke for field support. We thank K. Lewis and G. Robertson for advice and comments on capture-mark-recapture R code, and further thanks to G. Pearcy, for facilitating SIMS analysis.

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6.9 Appendix

Appendix 6.1. Mark validation trial to assess the retention and success of batch marking juvenile cod otoliths with three different fluorescein markers (alizarin red-S, calcein, tetracycline).

Methods

We conducted a mark-validation test from 17 August 2016 to 18 August 2016. Age-0 Greenland cod (*Gadus macrocephalus ogac*) were used for the mark-validation test because they were more abundant, and representative of the anticipated size of Atlantic cod (*G. morhua*) when marked in October. Test concentrations were 100 mg/L, 250 mg/L, and 400 mg/L for alizarin red-S (Blom *et al.*, 1994; Lü *et al.*, 2014b), 250 mg/L, 350 mg/L, and 500 mg/L for tetracycline (Monaghan, 1993; Lü *et al.*, 2014a), and 50 mg/L, 150 mg/L, and 250 mg/L for calcein (Wilson *et al.*, 1987; Monaghan, 1993). We placed 10 fish in each of nine 18-L plastic containers as tanks, set up inside the three 120-L plastic totes, with different alizarin red S, calcein, and tetracycline concentrations in each tank. We selected the lowest dye concentration that produced a visible mark for the experiment.

Results

Atlantic cod (*Gadus morhua*) were not settled in large numbers during the time of the mark validation study. Therefore, mark validation was primarily conducted using readily available Greenland cod (*Gadus ogac*, n= 78) in August 2016. Mortality occurred in all three alizarin red S levels. Mortality was highest in the 400 mg/L treatment (6 of 11 individuals), followed by the 250 mg/L treatment (5 of 11 individuals), and the lowest was at the 100 mg/L treatment (4 of 11 individuals). Temperature during the marking period in the marking tanks averaged 10.7 °C, while the mean water temperature in the sound was 13.5 °C. The change in temperature from field to tank may be a large factor in high mortality rates. The difference in temperature between the tanks and the field was corrected for the mark recapture study in October. The highest mortality in calcien (6 of 10 individuals) in the 150 mg/L treatment compared to 3 of 10 individuals in the 50 mg/L treatment (n=3). However, we cannot fully attribute mortality to the treatment given the warm water temperatures (10.5 °C). Alizarin red S and caclein marks were present on all otoliths. The lowest alizarin red S treatment (100 mg/L), yielded visible, but weak, marks. We therefore opted to use the intermediate level of 250 mg/L. Because calcien marks were strong for all otolith treatments, we selected the lowest concentration of 50 mg/L. Of the marked fish, there were two Atlantic cod that had been collected and were successfully marked with Calcein. Tetracycline had the highest mortality rate, with 12 out of 16 mortalities for 250 mg/L treatment, and 3 out of 11 mortalities for the 350 mg/L treatment.

Data on marks detected through subsampled fish in October are available at https://doi.org/10.5683/SP3/NPQSLV.

Appendix 6.2. References on the use of fluorescent markers to batch mark juvenile fish.

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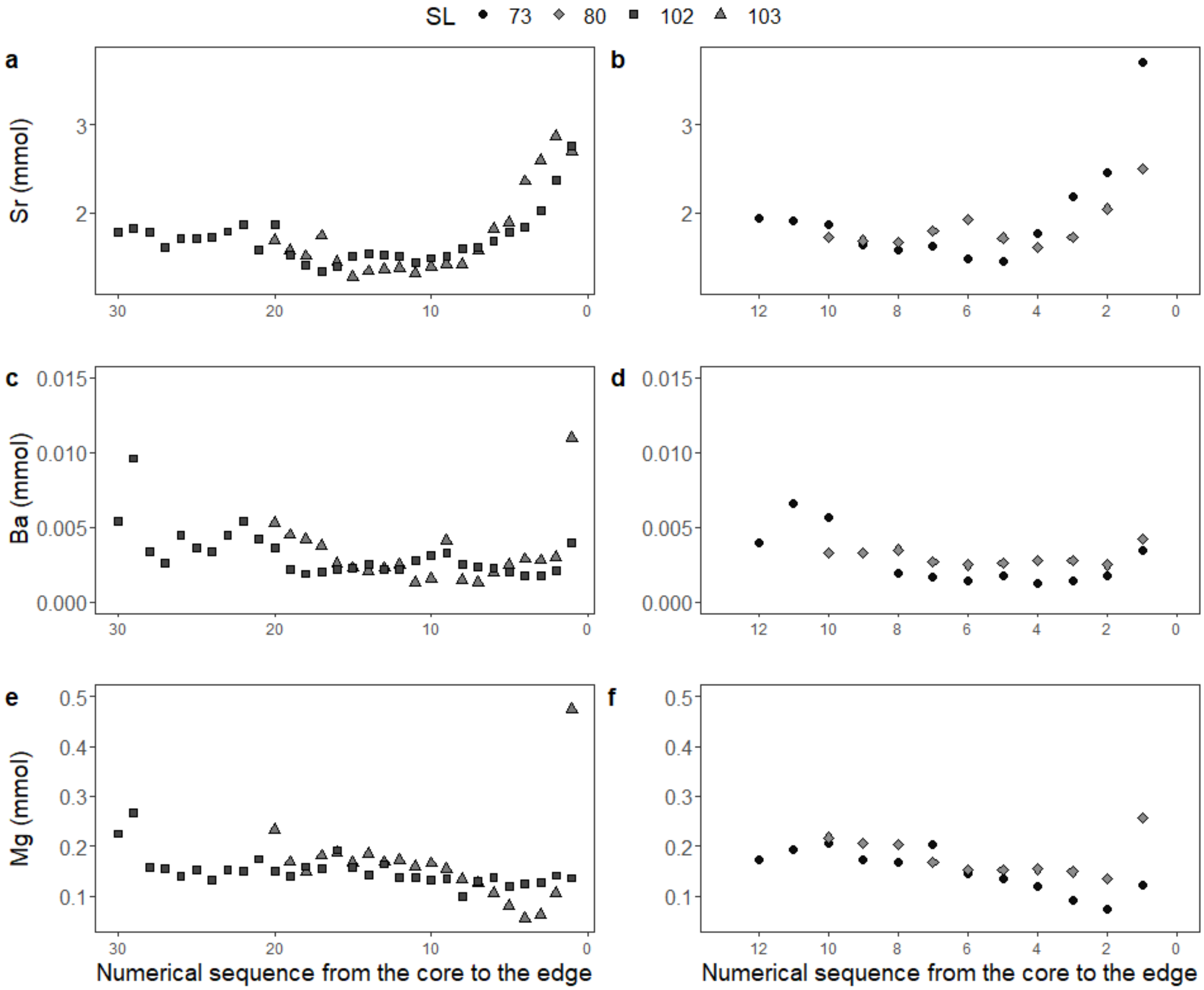

Appendix 6.3. Trace element cross section of a subsample of juvenile Atlantic cod sagittal otoliths under the same temperature and salinity treatments from October 2016 to April 2017 using secondary ion mass spectrometry (SIMS). Points represent sections along the otolith from the nucleus to the edge. Pulse 1 fish are 102 mm and 103 mm SL, respectively; and Pulse 2 fish are 73 mm and 80 mm SL, respectively.

Appendix 6.4. Analysis of Deviance (ANODEV) of change in Mg trace elements (mmol) in relation to pulse, season, and site. Analysed using a generalized linear mixed effect model (GLMM) with Gamma distribution and log link and fish ID as a random effect. Table contains the parameter, Chi-square statistic (Chisq), degrees of freedom (Df) and P-value.

Parameter	**Chisq**	**Df**	**p-value**
Intercept	186.6209	1	$<2.2 \times 10^{-16}$
Pulse	3.0055	1	0.08298
Season	35.2797	1	2.856×10^{-9}
Site	5.0679	2	0.07935

Appendix 6.5. Analysis of Deviance (ANODEV) of change in Ba trace elements (mmol) in relation to pulse, season, and site. Analysed using a generalized linear mixed effect model (GLMM) with Gamma distribution and log link and fish ID as a random effect. Table contains the parameter, Chi-square statistic (Chisq), degrees of freedom (Df) and P-value.

Parameter	**Chisq**	**Df**	**p-value**
Intercept	2043.07	1	$<2.2 \times 10^{-16}$
Pulse	1.2929	1	0.2555
Season	24.5490	1	7.245×10^{-7}
Site	0.4118	2	0.8139

Appendix 6.6. Analysis of Deviance (ANODEV) of change in Sr trace elements (mmol) in relation to pulse, season, and site. Analysed using a generalized linear mixed effect model (GLMM) with Gamma distribution and log link and fish ID as a random effect. Table contains the parameter, Chi-square statistic (Chisq), degrees of freedom (Df) and P-value.

Parameter	**Chisq**	**Df**	**p-value**
Intercept	137.7917	1	$<2.0 \times 10^{-16}$
Pulse	0.0701	1	0.79116
Season	3.2101	1	0.07318
Site	0.3835	2	0.82553

Chapter 7 – Thesis conclusions

7.1 Overview

In this dissertation, I have focused on winter survival of juveniles during their first year of life, as it was previously considered a survival bottleneck due to potential food limitation and cold temperatures. Natural mortality varies across life stages, species, and regions (Chapter 2). My specific aims in this dissertation were to evaluate overwinter mortality in age 0-1 Atlantic cod by considering the role of size, body condition, food availability, and winter duration. Additionally, I conducted a field-based capture-mark-recapture study to determine where age-0 cod reside during their first winter and whether estimates of mortality might be influenced by movement.

The results of this dissertation show that winter is not necessarily a survival bottleneck for age-0 cod under certain conditions. In contrast to my expectations, I found that mortality rates can be low in 47% of winters, with variable size-structured survival which is maintained across the winter period. During winter, mortality rates vary by recruitment pulses, with early pulses exhibiting high mortality in some years, and low mortality in others (Chapter 3). Small juveniles often have high survival probability (Chapter 4), but large juveniles can also exhibit very high winter survival rates (Chapter 6). The presence of food, even in small amounts, is important during winter, with modest amounts maximizing winter growth and condition potential for juvenile cod, whereas the absence of food results in increased mortality in small juveniles (Chapter 5). Lastly, this research highlights that the period leading up to winter is important for survival overwinter. High body condition in the fall indicates high winter survival probability (Chapter 4), and evidence of size-structured mortality (Chapter 6) indicates that the fall season is a critical period, rather than the winter.

7.2 Methodology

I used three inferences to assess overwinter survival in age 0-1 juvenile Atlantic cod. The combined use of long-term datasets, an experimental study, and a field study allowed me to break a system of complex problems into component parts which could be investigated in detail separately. Long-term datasets showed patterns that might otherwise be missed in 2-3 field seasons of a typical PhD thesis. The experimental study complimented my time series analyses and allowed me to test specific questions in a controlled setting. Finally, my field study allowed me to assess survival in a natural setting, often an omitted component of predominantly lab, modelling, and time-series inquiry.

Ecological studies demand multiple modes of inference because each study comes with a set of limitations and assumptions. Winter classifications between chapters offers a primary example of limitations. In Chapter 4, I defined winter based on temperature characteristics, but availability of fish in the coastal zone limited sampling to months before and after winter. In Chapter 5, I defined winter onset in January, the average start time based on temperature profiles. Additionally, I defined the end of winter based on fish health rather than water temperature. Lastly, Chapter 6 utilized a different winter classification based on feasibility of marking and releasing juvenile fish before they moved away from eelgrass zones. Instead of assessing mortality from December to May, I had to assess mortality from end of October to May. Additional assumptions in interpreting field results must also account for emigration, immigration, and predation. In contrast, laboratory studies limit behavioural traits, such as predator avoidance, and cannot always be directly applied to field applications. Chapter 5 showed that in the presence of food, juvenile fish can maintain and increase growth. However, the experiment did not account for foraging behaviour in the presence of predators. In a field situation, juveniles may decide to forage for food based on perceived risk levels. Additionally, perceived risk may change under different temperature regimes. In contrast, I observed low winter mortality in Chapter 6. Low mortality in one year does not mean low mortality in all years. However, it does illustrate that juveniles can survive in ideal conditions. For this reason, studies using long-term datasets (Chapter 4) are important because they allow us to evaluate trends overtime. Use of long-term data also brings additional assumptions such as sampling intervals, catchability, and biotic and abiotic variables.

Finite mixture distribution models provided an important tool facilitating my investigation of fine-scale population dynamics in fish populations with multiple recruitment pulses. Mixture distribution models assisted pulse assignment for age-0 and age-1 cod and provided the basis of size-structured analysis throughout my dissertation. Pulse structure is an important component of population dynamics for fishes that settle multiple times throughout a year (Methven and Bajdik, 1994; Geffen *et al.*, 2011; Dolan *et al.*, 2021). Recognizing the development and assignment of each pulse allowed me to investigate winter survival dynamics at a fine population scale (i.e., sub-annual).

Fulton's condition factor K was my metric of choice throughout my dissertation. Condition factors can function as indicators of energy content in fish and have been used extensively in Atlantic cod research (e.g., Lambert and Dutil, 1997) and can be used to identify large-scale seasonal differences in the body condition of populations (Wuenschel *et al.*, 2019). Fulton's K is also a simple index which requires minimal measurements and resources, allowing comparisons across multiple studies and life stages, and can indicate where higher resolution condition metrics (e.g., lipid analyses, bomb calorimetry, etc.) might be useful.

7.3 Implications

My main results show that large body size does not always infer a survival advantage, and that winter can result in high survival. These results contradict previous assumptions. In freshwater systems, larger fish have a survival advantage noting typical overwinter food limitation. Marine systems provide a unique ecosystem, with seasonal fluctuations in food, multiple plankton blooms, seasonal thermoclines, and habitat shifts. Until now, we believed that marine winter dynamics would mirror those of freshwater dynamics based on fish physiology, metabolism, and bioenergetics. Instead, I have found greater complexity in size-structured survival. High winter survival with advantages to small body size could be influenced by, but not limited to, seasonal food availability, predator abundance, predator/prey size ratios, temperature refuges, and complex size classes. Winter research should continue across sub-arctic and arctic regions to determine if these survival patterns are consistent across multiple regions and populations.

Size structure in populations plays an important role in juvenile fish survival rates in multi-pulsed populations (Geffen *et al.*, 2011). My research showed substantial variability in this size-structured population – some years exhibited high survival among large age 0 fish; in contrast other years exhibited high survival among small fish (Chapter 3). The year-to-year variability in pulse survival over winter was consistent with a bet-hedging strategy in cod, associated with protracted spawning period (Secor, 2007). Bet-hedging is often highlighted during the spawning and egg stage, but limited research has assessed bet-hedging at the juvenile stage (see Dolan *et al.*, 2021). The variable survival I observed across pulses supports the inherent natural variability in mortality rates, not only across species and life stages, but within them.

Food obviously plays an important role in survival of fishes, both leading up to and throughout the winter period. However, I observed high winter survival when condition entering winter was high compared to when condition was low (Geissinger *et al.*, *submitted*). Further, even small amounts of food enhanced juvenile survival significantly throughout the winter months (Geissinger *et al.,* 2021). Some juveniles had high post-winter condition, indicating that there was sufficient food throughout the winter months (Geissinger *et al.*, 2022). In cases where there might be low levels of food, condition and body size leading into winter will promote high survival.

The variable size-structured survival I have shown throughout my dissertation highlights the importance of studying multiple biotic and abiotic variables to better explain natural mortality. Size has a limited effect during winters in instances when resources are available. Juvenile fish can use the fall season to consume food and build up energy reserves to increase their probability of survival over winter. Juvenile cod experience high predation post-settlement (Linehan *et al.*, 2001; Laurel *et al.*, 2003). However, juveniles may have a high chance of surviving winter if they are able to evade predators throughout the fall. While winter may be considered a harsh environment, it may provide a stable refuge for juvenile fish from predators, many of whom are quite possibly inactive at this time, compared to the fall. Juvenile cod can cope with colder temperatures more easily than their piscivorous larger conspecifics (Goddard *et al.*, 1992) and other predators. Additionally, juveniles may, at times, have abundant food and/or be able to forage without threat of predators, as the predators may move to deeper, warmer water. In contrast to stable winters, fall seasons are more dynamic, with large temperature fluctuations and high predation risk. The importance of high body condition means that juveniles may have to take risks to find food, which increases susceptibility to predation (Halpin, 2000; Biro *et al.*, 2005). Winter may provide a stable refuge for juveniles but fall appears to be a critical period to grow and store energy, while evading predators prior to winter.

There has been a shift in focus on juvenile life stages across multiple ecosystems (Ottersen *et al.*, 2014; Laurel *et al.*, 2016; Lunzmann-Cooke *et al.*, 2021). The juvenile life stage can be heavily influenced by temperature. The recent North Pacific marine heatwave has led to recruitment failures (Litzow *et al.*, 2022), change in growth conditions (Blaisdell *et al.*, 2021), and change in food availability (Rogers *et al.*, 2021) in several species. These cases are mere examples of warming events; similar changes could also occur elsewhere in the world, due to global climate changes. In the case of juvenile Atlantic cod, warmer, shorter winters would provide additional stress on individuals (increased metabolism, change in food availability). Energetics plays a substantial role in interannual survival. The added importance of energy acquisition and storage prior to and during winter which I have identified in my results can determine a cohort's ability to survive (Heintz and Vollenweider, 2010; Sewall *et al.*, 2019; Geissinger *et al.*, 2021). In subarctic coastal habitats a juvenile fish's ability to store energy in the fall period could be critical.

7.4 Future directions

My research on overwinter survival of juvenile cod is an important stepping-stone to understand the transition from age-0 to age-1 juveniles in a marine ecosystem. My results point to fall as a critical period for juvenile fishes. Building on my research, I propose the following future studies:

7.4.1 Diet

The period before winter appears to be critical for survival through the first winter, and quality of food may play an important role in overwinter survival. Food sources from eelgrass habitats have been shown to be of low lipid quality (Copeman *et al.*, 2008). However, juvenile pulses settling in December (<45 mm SL) have survived through winter in some years. Juvenile cod – similar to other species – may consume different quality food sources based on their settlement time (Sogard and Able, 1992; Dolan *et al.*, 2021), which my results would suggest influence winter survival. The amount and quality of food for age-0 cod in Newfoundland remains poorly understood. We do not know how much food is in the system, how food varies seasonally and annually, or the differences in food availability among recruitment pulses. Prey quality and shifts in availability throughout the fall and winter periods would reveal much to explain survival and population dynamics.

7.4.2 Bioenergetics

In addition to understanding food consumption and availability, understanding how juvenile fish use their consumed food (i.e., where is the energy stored, what type, quality, etc.) is equally important. Intensive diet studies will be valuable indications of bottom-up processes which are strong predictors for population trajectories (Buren *et al.*, 2014). Similar to research conducted on other northern species (Farley *et al.*, 2016; Copeman *et al.*, 2017; Sewall *et al.*, 2019), bioenergetic studies in coastal Newfoundland would allow us to compare across coastal zones, ecosystems and species (Jørgensen *et al.*, 2016), providing synoptic evidence of patterns in similar ecosystems.

7.4.3 Linking diet to oceanographic processes

The bio-physical relationship in aquatic systems is often overlooked when discussing survival of juvenile fish. Fjord ecosystems provide important nursery habitats for many fish, with high productivity, isolation, and habitat complexity compared to oceanic waters nearby (Wennhage and Pihl, 2001; Aure *et al.*, 2007; Renkawitz *et al.*, 2011; Gilmartin, 2017; Meire *et al.*, 2017). As stated previously, diet likely plays an important role in juvenile dynamics, and phytoplankton blooms in coastal nurseries may provide important sources of high-quality food before the onset of winter. The role of phytoplankton (through zooplankton) in the nutrition of juvenile Atlantic cod has not been determined in the Northwest Atlantic. Understanding the relationships between oceanographic processes in coastal systems and how they influence biological conditions for cod could improve our ability to anticipate the effects of changes in climate on these ecosystems.

7.4.4 Predator-prey dynamics

The behavioral component of winter survival in juvenile fish in the presence and absence of predators represents a critical research area. Future studies should consider temperature-dependent predation, predator windows, and temperature-dependent foraging. Many marine fish populations provide an added complication with cannibalism, which can occur within the same age-class. Future predator-prey research should combine field and laboratory studies in order to understand behavior dynamics more fully in isolation and in practice.

7.5 References

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